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THE UNIVERSITY OF ALBERTA

FEEDING AND BEHAVIOR OF NORTHERN PIKE (*Esox lucius* Linnaeus)

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1976

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Feeding and Behavior of Northern Pike (Esox lucius Linnaeus)" submitted by David Gordon Christiansen in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor

Kenneth B. Armitage

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Date 22 Oct. 1976

ABSTRACT

The growth, feeding, and predatory and social behavior of northern pike (Esox lucius L.) in Kakisa Lake, Northwest Territories were examined during the summers of 1973 and 1974.

The growth rates of northern pike from Kakisa Lake were found to be substantially higher than those of fish from Great Slave Lake, Northwest Territories. Female northern pike displayed higher growth rates than males of the same age, following sexual maturation. Females had significantly greater average jaw widths than males of the same fork length.

The northern pike of Kakisa Lake were mainly piscivorous, but in the spring their diet included large numbers of invertebrates. The diet composition of northern pike showed seasonal changes, which were a result of changes in the relative abundance of the various prey species, and also the occurrence of a spring spawning fast. Northern pike exhibited size selective predation, and this was reflected in changes in the diet composition with increase in predator size. Female northern pike consumed prey fish of greater body size than male northern pike of the same fork length.

Northern pike displayed two types of predatory behavior, with the stalking form of predation being more successful than the pursuit form. The use of stalking predation depended largely on the availability of adequate cover in which the predator could remain hidden until prey had moved close. Behavior of prey fish was the main factor controlling the occurrence and the type of predation used by northern pike. The outcome of a predatory act dictated the subsequent activity undertaken by northern pike. The overall predatory strategy of northern pike is one of efficient use of opportunities in a manner which minimizes energy expenditure.

Northern pike were basically solitary, but did enter into agonistic, neutral, and positive social interactions. Northern pike exhibited a limited repertoire of agonistic displays, most of which appeared to arise from basic predatory movements. Agonistic interactions also took the form of size-related avoidance behavior. Physical combat did not occur between northern pike. The social structure was largely based on individual distance requirements, but temporary site use and range restriction also existed. Habitat preferences were shown. Food deprivation increased aggressiveness, and decreased activity and social tolerance of northern pike.

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INTRODUCTION

The northern pike (Esox lucius L.) is resident in most freshwater lakes and streams throughout the northern hemisphere, where it occupies the position of an upper level piscivore.

Numerous studies have dealt with the general ecology and breeding biology of northern pike. There is, however, a paucity of information pertaining to the behavior of the species, especially under natural conditions. Most behavioral studies have dealt with the spawning activities of northern pike, or have been conducted in artificial situations.

The objectives of the present study were to observe and describe the postspawning behavior of northern pike - under field conditions - as it relates to predation, intraspecific interactions, and general activity patterns. Examination of feeding habits was also implemented to provide information on the existing predator-prey relationships of the Kakisa Lake population. The work reported here mainly pertains to adult northern pike; some incidental observations of juveniles are included and will be labeled as such.

The piscivorous propensities of northern pike have been well documented by Frost (1954), Crossman (1962), Seaburg and Moyle (1964), Lawler (1965), Hunt (1965), Johnson (1969), and others. Under certain conditions the diet of northern pike may include invertebrates (Johnson, 1969; Lamoureux, 1973), waterfowl (Solman, 1945; Lagler, 1956), and small terrestrial and semiaquatic vertebrates (Scott and Crossman, 1973). Northern pike populations typically contain a high percentage of individuals with empty stomachs at any one time (Allen, 1939). Lawler (1965) finds Heming Lake northern pike to exhibit the highest percentage of stomachs empty during June, July, and August. Allen (1939) states that lowest levels of feeding occur in winter in the Lake Windermere population; Frost (1954) suggests that this same population feeds least during the spring period as a result of a spawning fast by adults. However, the existence of a spawning fast has been subsequently denied by Healy (1956) and others (see Toner, 1969). This conflicting information may be a result of alterations in the feeding habits of northern pike in response to changes in prey abundance, as described by Ivanova (1969). It may also be necessary to take into account the rate of digestion of prey at different times of the year, if the percent of stomachs empty is to be used as an index of feeding rate. Molnar and Tamassay (1967) have found large numbers of pike-perch (Lucioperca lucioperca) with full stomachs in the winter, but this they attribute to a much lower digestion rate and not to a larger ration at this time.

There is general agreement, in the more recent literature, that northern pike have fairly low maintenance requirements, and are relatively efficient converters of food (Johnson, 1966a; Carlander, 1969). Ivanova (1969) suggests that females begin feeding earlier in the spring than males, which she attributes to the fact that females leave the spawning grounds before males. Higher feeding rates of post-spawning females are believed by Makowecki (1973) to be the ultimate cause of the sexual dimorphism in body size of northern pike. He postulates that females are more aggressive following spawning (females are in poorer condition, since more energy is expended in eggs than in sperm), and hence can exclude males from prime spring feeding areas.

Prey selection by northern pike has been discussed in a number of studies. Frost (1954), Johnson (1959), and Johnson (1966b) conclude that prey selection does not occur, but that northern pike feed only on what is abundant and available. This is in disagreement with the findings of Hoogland et al. (1956), Beyerle and Williams (1968), and Mauck and Coble (1971), who all report prey selection occurring during feeding experiments. The problem, in part, appears to be semantic in nature, caused by variations in definition of the term 'selective'. The importance of preferred prey size is stressed by Baerends (1957), Ivlev (1961), Carlander (1969), and Coble (1973). Coble (1973) finds no influence of prey color or form on food selection by northern pike. The findings of Baerends (1957), Beyerle and Williams (1968), and Ivanova (1969) indicate the importance of prey behavior in controlling the predatory response. Hoogland _et al_. (1956), and Mauck and Coble (1971) conclude that northern pike prefer soft-rayed species of prey fish to spiny-rayed species.

The predatory act of northern pike has been examined and described by Wunder (1927), Hoogland _et al_.(1956), and Nursall (1973). Hoogland _et al_. (1956) divide the predatory act into seven distinct segments. These segments have been examined and revised by Nursall (1973). Nikolsky (1963) postulates that northern pike depend primarily on mechanical stimuli to detect prey, "while the function of the visual system is secondary and compensatory". Hoogland _et al_. (1956) suggest that "the perception of a fish from a distance greater than the 'leaping distance' is entirely visual". Northern pike visually examine prey for variable lengths of time before striking (Nursall, 1973). It is postulated by McNamara (1937) that the sense of olfaction may be used by northern pike in tracking other fish. Mauck and Coble (1971) examine prey vulnerability at different water turbidities and find no significant differences. They do state that diseased or injured prey are more vulnerable to predation. Frost and Kipling (1967) find that northern pike will not strike dead prey, even when it is artificially moved by water currents. Mauck and Coble (1971) conclude, from experiments in tanks, that cover does not alter vulnerability of prey to northern pike predation. Nursall (1973) reports a 41% success rate in predatory attempts of northern pike.

Available information pertaining to interactions between northern pike has largely been derived from observations of spawning fish. The most detailed study of spawning behavior is that of Fabricius and Gustafson (1958); other studies of this subject are those of Svardson (1948), Hampton (1948), and Clark (1950). During the spawning run male northern pike move into the spawning area first, traveling through the shallows and resting for extended periods between grass tussocks (Fabricius and Gustafson, 1958). These resting spots are not considered to be the centers of territories, since the fish do not return to them regularly. Fabricius and Gustafson (1958) postulate that spawning territories would not be held by northern pike, since it would be more advantageous to spread the high number of eggs over a large area. They also report observations of agonistic displays between males (on the spawning grounds), which they describe as "... a characteristic threat posture, in which the branchiostegal membrane is lowered ...". Fabricius and Gustafson (1958) also note head shaking movements used by unripe females to repulse courting males. Frost and Kipling (1967) observe that juvenile northern pike remain a discrete distance from one another, but do not exhibit site attachment or territory defence. These workers describe instances when tail nipping, chasing, and cannibalism occur in tanks containing fry at high densities. At low densities aggression is almost non-existent in these same populations. Frost and Kipling (1967) conclude that northern pike fry require a buffer area around themselves, which if denied, will result in aggression.

Studies of activity patterns indicate that these fish tend to be crepuscular in nature (Lawler, 1969; Poddubnyi, 1970). Carlander (1949) indicates that gill net catches are highest in the morning (0800 to 1000 hours), with a second slight peak in midafternoon. Radio tracking studies suggest the existence of three activity peaks during a 24 hour period (Malinin, 1971). These are the dawn and dusk activity periods, and a third slightly smaller one at midday. Alterations of normal daily activity patterns may be caused by certain environmental changes. Buss (1961) determines that northern pike activity and feeding is curtailed when water temperatures exceed the optimum (approximately 25 to 27°C). Fabricius and Gustafson (1958) document curtailment of spawning activities coincident with short periods of lower than normal spring water temperatures. Malinin (1971) reports different levels of activity on bright versus cloudy days. He also suggests that northern pike can detect pending weather changes, since general movements of fish to deeper water occur prior to storms and wind direction changes.

In general, it appears that northern pike are solitary predators, which become aggressive if approached by conspecifics. They seem to show a daily and seasonal cycle of activity and related feeding. These predators apparently detect prey mainly by sight, and are opportunistic in their feeding habits. Information is lacking on the social behavior of adult northern pike outside of the breeding season, and the social structure of northern pike populations has not been clearly described.

DESCRIPTION OF STUDY AREA

I Lake

Location

Kakisa Lake is located in the Northwest Territories at latitude 60° 50' and longitude 117° 40'. It is approximately 100 km due west of the town of Hay River (Figure 1).

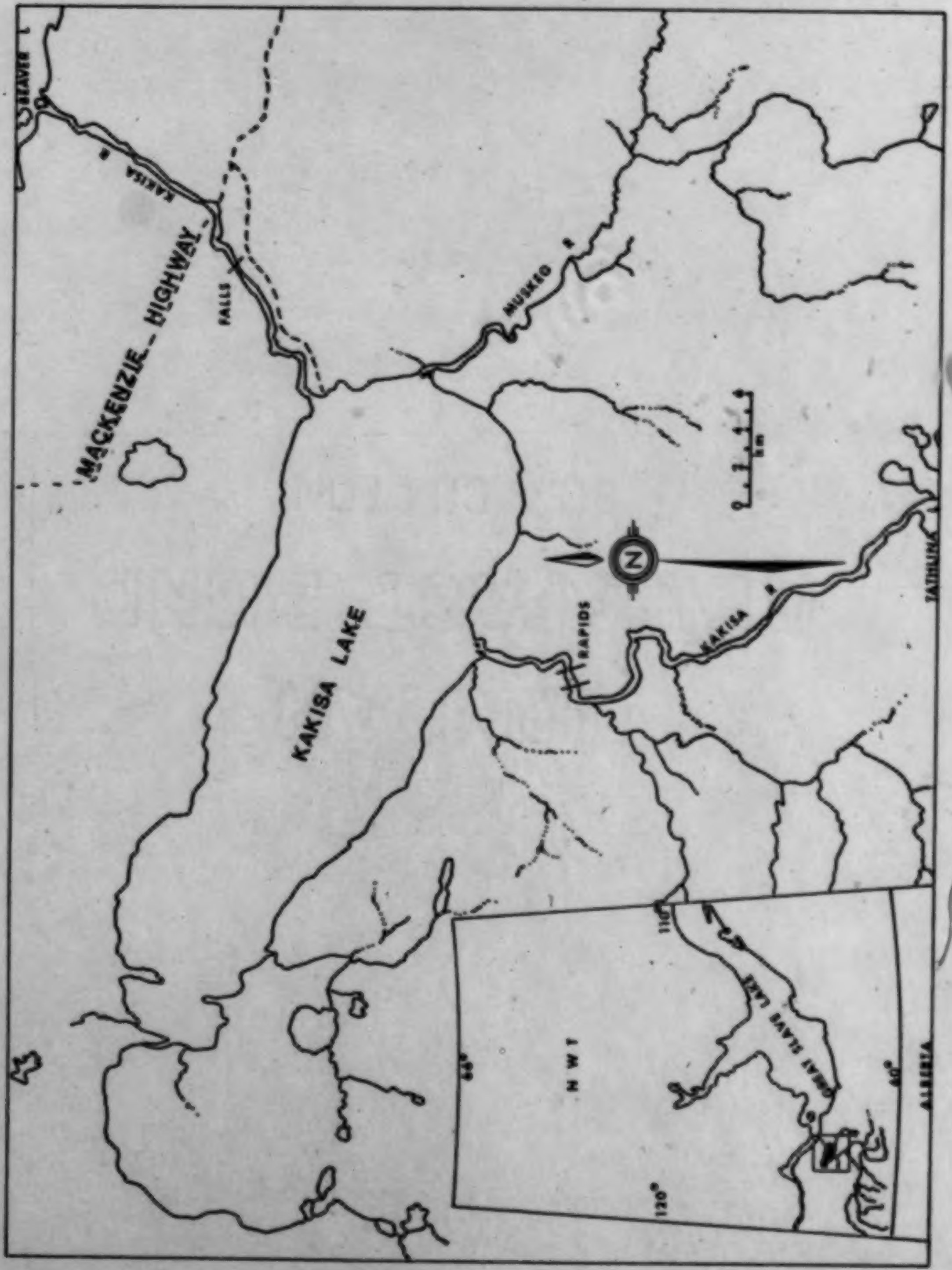
Topography

The lake lies at elevation 221.5 m above sea level, on a plateau between two parallel escarpments. One escarpment drops steeply to form the south shore of the lake, the other lies to the north between Kakisa and Great Slave Lakes. The north, east, and west shores, unlike the south shore, rise only slightly before becoming flat at elevation 223.5 m (approximately) above sea level. These low lying areas are poorly drained, and hence most of the terrain is covered by muskeg and bog. The south shore, being steeper, is drier.

Drainage basin

Two large and five smaller streams drain into Kakisa Lake (Figure 1). The Kakisa River, the major tributary, enters from the south via Tathlina Lake. This stream drains an area of approximately 4200 km^2, which extends south to

Figure 1. Map of Kakisa Lake and its drainage basin. Inset indicates the position of Kakisa Lake in relation to Great Slave Lake N.W.T.. Longitude and latitude indicated on inset.


MACKENZIE HIGHWAY
BEAVER
KAKISA R
FALLS
MUSKEG R
KAKISA LAKE
RAPIDS
KAKISA R
TATHLINA
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0
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N W T
GREAT SLAVE LAKE
62°
110°
120°
60°
ALBERTA

near the N.W.T. - Alberta border. The gradient is much higher than that of the other tributaries, and the stream tends to remain turbid throughout the entire open water period. The Muskeg River is the second major tributary; it flows in from the southeast. It is approximately 48 km in length, and is more meandering and slow flowing than the Kakisa River (Figure 1). The Muskeg River drains extensive, low-lying areas of muskeg, and as a result is transparent while being tea-colored. The five minor tributaries (Figure 1) are short, slow flowing streams with very small watersheds. These streams all drain muskeg areas; their features are similar to those of the Muskeg River.

The outflow is the Kakisa River (Lower Kakisa River, for this thesis). It flows northward emptying into the lower end of Great Slave Lake at the head of the Mackenzie River (Figure 1). Along its 25.7 km length the Lower Kakisa River drops precipitously over several minor rifts and the escarpment at Lady Evelyn Falls.

Basin morphology

Kakisa Lake is roughly rectangular, with a maximum length of 37 km and a maximum width of 11.4 km. The long axis is oriented in an east-west direction, along the path of the prevailing winds.

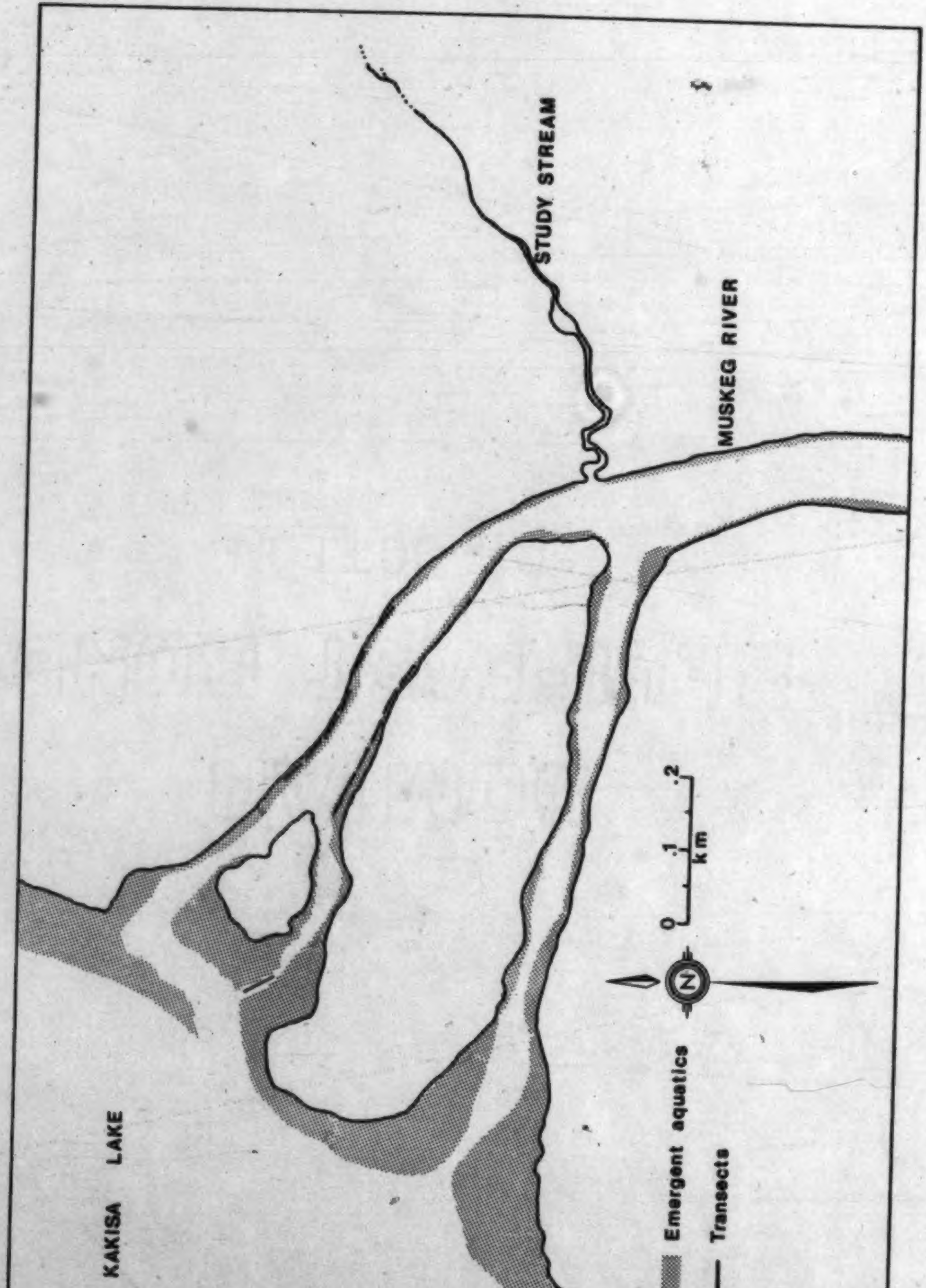
The lake basin is very shallow and regular, with gently sloping littoral areas. The depth contours follow a regular concentric pattern to a maximum of six meters. Lamoureux (1973) reports that the three to four meter depth zone is the largest, comprising 34.1% of the 332 km^2 area of the lake. Littoral areas comprise about 15% of the lake area. Most of the littoral zone (maximum depth 2.5 m) has a sand and gravel bottom, except for the alluvial silt regions off the river mouths. Below a depth of 3.0 to 3.5 m the bottom changes to a muddy, silt type sediment (Lamoureux, 1973).

Aquatic vegetation

Potamogeton richardsonii is the most abundant aquatic macrophyte, with associated beds of *P. pectinatus* interspersed throughout the littoral zone of Kakisa Lake (Lamoureux, 1973). Because of wave action, most emergent vegetation is restricted to semiprotected bays and river mouths. In these areas *Carex* and *Equisetum* belts extend from shore into the shallows to a depth of about 0.3 m. Outside this belt *Scirpus* dominates the emergent zone to a depth of 1.0 to 1.3 m. Small clones of *Typha* occur randomly within the *Scirpus* beds. Along channels at the river mouths, mats of *Nuphar* form a narrow 3.0 m wide band along the outer edges of the *Scirpus* beds.

The area around the mouth of the Muskeg River (Figure 2) has the largest beds of emergent vegetation in the east end of the lake. These plants extend several kilometers up this

Figure 2. Map of Muskeg River mouth and associated emergent aquatic macrophyte beds. Study Stream position and transect lines are also indicated.


KAKISA LAKE
STUDY STREAM
MUSKEG RIVER
Emergent aquatics
Transects
0
.1
.2
km
N

river as narrow bands 8.0 to 10.0 m wide along both banks, providing excellent spawning habitat for northern pike.

Fish species

A list of the fish species of Kakisa Lake, and their estimated relative abundances, is given in Appendix 1.

Climate

The climate of the area is typical of northern boreal regions; with cold, long winters and brief, hot summers. The average annual percipitation of the region is approximately 32.0 cm.

Lamoureux (1973) gives a detailed description of the general features of Kakisa Lake and its environs.

II Description of Study Stream

A small tributary of the Muskeg River (Study Stream) was selected as the site for behavior observations. An observation area was established on this tributary approximately 100 m upstream from the Muskeg River. The Study Stream flows southward, and enters the Muskeg River one kilometer above its entrance into Kakisa Lake (Figure 2).

During spring runoff the discharge of the Study Stream is approximately 0.01 m^3/s, but later in the summer this flow almost ceases. Summer stagnation is prevented by higher water levels in Kakisa Lake; these back up the Muskeg River into the lower 200 m of the Study Stream.

Salix is the dominant tree lining the low banks of the Study Stream, in some areas extending over the water. Carex and Equisetum form the riparian understory, which extends into the stream to a depth of up to 0.4 m. Floating mats of Sagittaria are located in slackwater on bends of the stream. In midsummer the deeper pools show growths of Myriophyllum exalbescens and Ceratophyllum demersum, with small mats of Sparganium present.

The Study Stream is a natural spawning area for northern pike. Fry hatched in the observation area, and a number of adults congregated below the observation area during the spawning run.

Invertebrates occurring in the Study Stream are similar to those of the Muskeg River, as described by Lamoureux (1973). Numerous dipterans of the families Culicidae, Tendipedidae, and Tabanidae are present as larvae. In addition, odonatans, coleopterans, trichopterans, and ephemeropterans of various species inhabit the Study Stream.

MATERIALS AND METHODS

I Physical and Chemical

Dissolved oxygen samples, water chemistry samples, and water temperature readings were taken in three general areas (Kakisa Lake, Muskeg River, and Study Stream) for comparative purposes. Dissolved oxygen samples were analysed in the field using the Alsterberg (Azide) modification of the Winkler method. One liter water samples were collected on a bimonthly basis. These were fixed with 5.0 ml of chloroform, frozen, and analysed later in the Department of Zoology Water Laboratory, at The University of Alberta. Daily surface temperature readings were taken with a Bistabil-Eterna mercury thermometer. Temperature profile readings were made at the lake station with an ET100 telethermometer (Applied Research, Austin, Texas). Additional temperature readings and Secchi disc readings were taken adjacent to gill net sets in the Lake.

A daily weather condition record was kept. Daily barometric pressure data were obtained from The University of Alberta Research Station, at Heart Lake, N.W.T., located approximately 45 km northeast of the study area.

II Biological

A. Limnological

Aquatic vegetation samples were collected from littoral areas of Kakisa Lake, the Muskeg River, and the Study Stream; these samples were identified, while fresh, using the keys of Ward and Whipple (1959) and Hotchkiss (1972).

Benthic invertebrate collections were made in open water areas using an Ekman dredge, and these were sieved in an Ekman bucket with a No. 20 mesh bottom. In areas of dense aquatic vegetation dipnet samples of invertebrates were collected. The samples were preserved in 10% formalin, and identified later using a dissecting microscope. The invertebrate keys of Pennak (1953) and Ward and Whipple (1959) were used. This material was used as a reference collection to be compared with invertebrates eaten by northern pike.

B. Fisheries

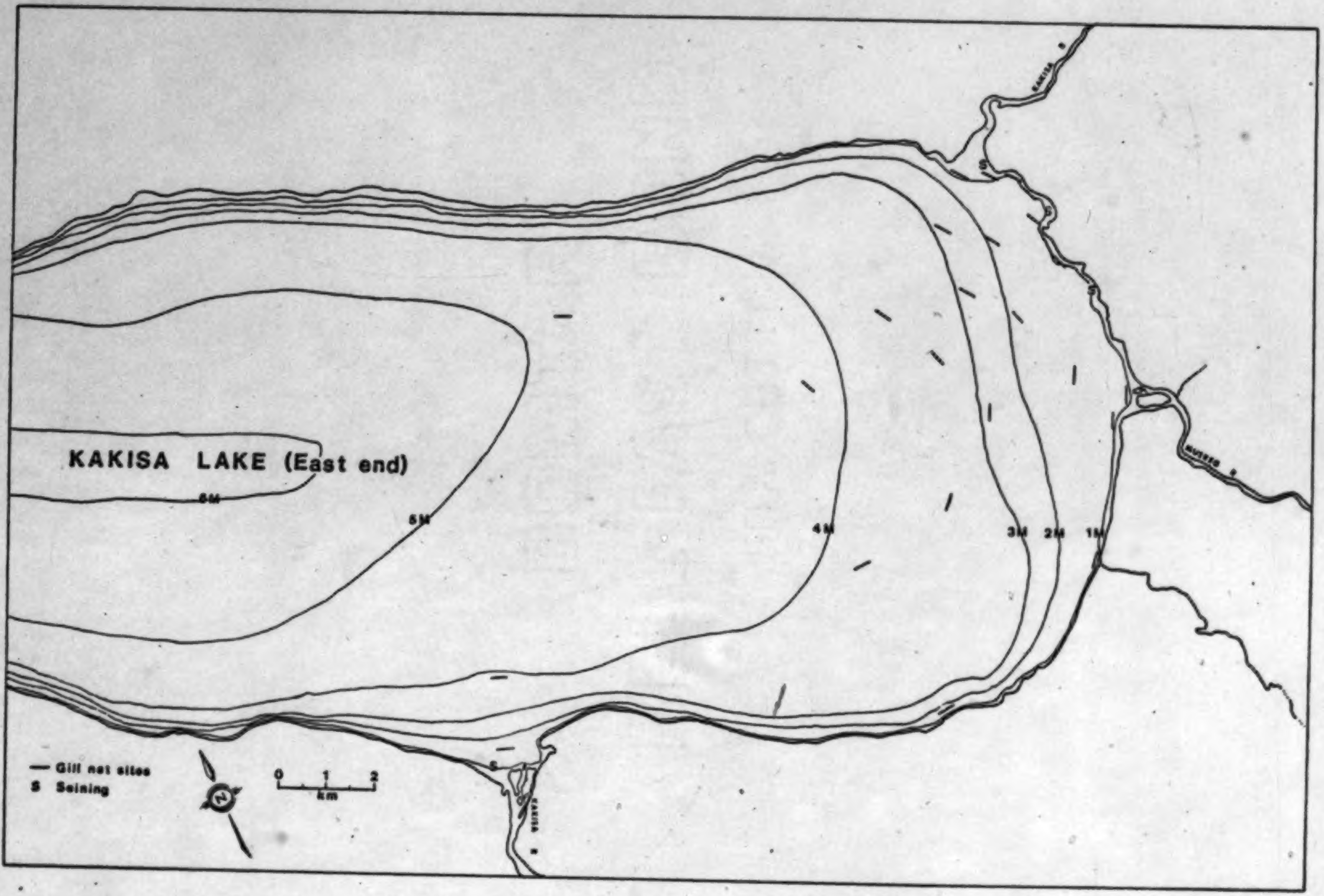
Fish collecting

Gillnetting, beach seining, dipnetting, trawling, and angling were used to obtain samples of fish species present in the lake.

Gillnets were set once a week in the east end of Kakisa Lake (Figure 3). A netting period lasted 24 hours. Two test gangs were usually set; one gang set in shallow water (zone of submergent aquatic vegetation) parallel to shore, and the other gang in deep water (outside vegetated zone). Standard test gangs were composed of four nets of different mesh sizes. Three nets in each gang were 18.3 m long by 2.4 m deep (38 mm, 64 mm, and 89 mm, stretch mesh), and the fourth net was 13.4 m long by 2.4 m deep (25 mm stretch mesh).

In special cases sets of 89 mm and 102 mm stretch mesh nets were made to collect northern pike for behavior tests. During the spring a number of northern pike were obtained from commercial fishermen on the Muskeg River. Beach seining was conducted in the shallows to a depth of about 1.5 m. Bag seines of 9.0 m and 4.5 m length were employed. Dip netting was utilized to capture forage fish in areas of dense aquatic vegetation. Forage fish, to be used as northern pike food, were obtained by trawling in open water areas at surface, midwater, and bottom. The trawl design was similar to that of Qadri (1960). The frame was built of 25 mm water pipe, onto which a 2.7 m long, plastic-screen bag was attached. The dimensions of the bag mouth were 1.2 m by 0.8 m. Angling was use to collect live northern pike for behavioral studies.

Figure 3. Map of the east end of Kakisa Lake showing depth contours at one meter intervals. Gill netting stations and beach seining sites are also indicated.


KAKISA LAKE (East end)
KAKISA R
KAKISA R
1M
2M
3M
4M
5M
6M
S
S
— Gill net sites
S Seining
N
0 1 2
km

Fish measurements

Fork length measurements were made to the nearest 0.5 cm on a one meter measuring board. Fish weights were taken to the nearest 5.0 gm with Pesola spring scales. Mouth width measurements were taken with a plastic ruler inserted across the inside of the slightly open mouth at the posterior angle of the jaws.

Scale samples were taken from the left side of northern pike just anterior and ventral to the dorsal fin. Ageing was done by compressing the scales between glass slides, and viewing with a dissecting microscope. Otoliths were also taken from northern pike, but these proved unsatisfactory for age determination.

Gut analysis

Northern pike stomachs were removed intact and immediately preserved in 25% formalin. These guts were later examined and classified as containing food, empty-distended, or empty-constricted. Food items were identified under a dissecting microscope. Organisms from each stomach were grouped according to species, blotted dry, and weighed on a Mettler P1200 electric balance (sensitive to 0.1 gm). The volume of each group of organisms from a stomach was obtained using the water displacement technique. Whenever possible (1974 samples only), the direction of swallowing of prey fish was also recorded. Prey fish were also examined for any major parasites.

A series of specimens of forage fish from Kakisa Lake were decayed for approximately 10 days, and then preserved in 10% formalin. These fish parts were then examined, and reference drawings made for use as aids in identification of stomach contents of northern pike.

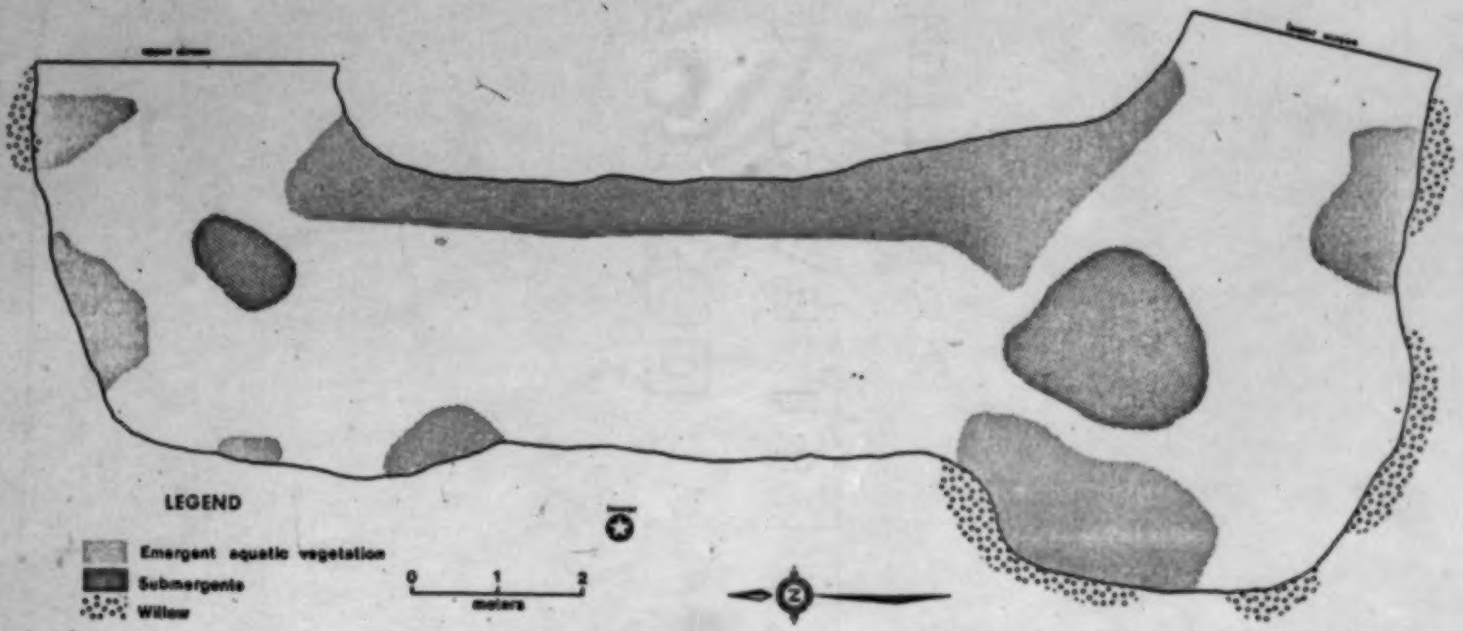
C. Behavioral Studies

Observation area

The observation area (Figure 4) was located on a bend of the Study Stream. The observation section was approximately 18.3 m in length. The maximum width was 5.8 m and the minimum was 3.4 m, giving a total surface area of approximately 61 m^2. A pool, 2.1 m in diameter and 0.8 m deep, formed the upper end of the enclosed section; a larger pool, 3.7 m in diameter and 1.2 m deep occurred at the lower end. A 10 m channel, 3.4 m wide and 0.6 m deep, joined the two pools. Natural aquatic vegetation was allowed to develop in the observation section of the Study Stream.

Barriers were constructed at the upper and lower end of the observation area to prevent the escape of fish. These barriers each consisted of a single log placed across

Figure 4. Map of observation area on the Study Stream. Emergent, submergent, and riparian vegetation areas indicated.


LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters

the stream from bank to bank, approximately 0.6 m above the water surface. A sheet of heavy plastic hardware cloth, firmly attached to the log on top, hung vertically to the stream bed. The bottom of this screen was covered with layers of rock and soil, as were the sides where they met the stream bank. This system allowed a normal flow of water, but provided effective barriers to fish movement out of the section.

An observation tower was built on the north bank of the stream halfway between the barriers. The observation platform rested atop a 3.0 m high tripod of aspen logs. Black plastic enclosed the sides of the platform, and green hardware cloth covered the front. Entrance was gained through a port in the rear of the enclosure. The location of the tower allowed a clear view of the entire observation channel.

Fish handling

Two galvanized steel stock-watering troughs were used as temporary holding tanks for fish destined for the observation channel. The troughs were 3.0 m long by 0.9 m wide by 0.75 m deep. Screen-covered openings near the bottom of the tanks allowed water passage. Wooden cradles supported the troughs, so that they were filled with water to a depth of 0.4 m. Hardware cloth covers were affixed to the top of the troughs to prevent escape of northern pike. The holding tanks were located in the Study Stream 80 m below the observation area.

Upon capture, northern pike were weighed to the nearest 5.0 gm, and fork length measurements were made. Sex was determined if fish were ripe; this was done by applying pressure to the abdominal region to produce gamete flow. For purposes of identification, the fish were tagged with colored strips of Dymo label tape. These were attached to a short length of monofilament line, which was passed through the dorsal musculature of the fish just slightly anteroventral to the origin of the dorsal fin. After processing, the northern pike were placed singly into the holding tanks. Following a sufficient recovery period (2 to 7 days) the fish were dipnetted from the holding tanks and transferred to the observation area.

Northern pike were selectively removed from the observation area by shooting with a 0.22 caliber rifle. Upon removal the fish were again weighed, measured, and finally necropsied. Scale samples and gut contents were also collected at this time.

Observation

Behavior observations were conducted from May through August of 1973 and 1974. Observations were restricted to the daylight hours. Observation days and time of day when observations occurred were randomly selected. One quarter of an hour was allowed to elapse between entrance into the tower and commencement of observations.

Detailed records were kept of the activities and behaviors of all northern pike visible during the observation period. Short-hand notes or cassette voice tapes were used to record observations. Activities were timed with a Marathon pocket watch. Polaroid sunglasses and 7 x 35 mm Bushnell wide angle binoculars were employed to increase acuity of observation. An alphanumeric coordinate grid pattern was applied to maps of the observation area to allow accurate description of fish positions (Appendix 2). By tracing fish movements on these maps it was possible to calculate the approximate distance of travel of individuals.

Prey fish added

Naturally occurring invertebrates and juvenile northern pike were initially present as prey in the observation area. Additional prey in the form of live forage fish were added at intervals during the study. Ten species were added as prey; trout-perch (*Percopsis omiscomaycus* (Walbaum)), spottail shiner (*Notropis hudsonius* (Clinton)), lake chub (*Couesius plumbeus* (Agassiz)), white sucker (*Catostomus commersoni* (Lacepede)), longnose sucker (*Catostomus catostomus* (Forster)), walleye (*Stizostedion vitreum* (Mitchill)), ninespine stickleback (*Pungitius pungitius* (L.)), slimy sculpin

(Cottus cognatus Richardson), burbot (Lota lota (L.)), and juvenile northern pike. Lake whitefish (Coregonus clupeaformis (Mitchill)) and cisco (Coregonus artedii Lesueur) were not used as prey, since it was extremely difficult to obtain live specimens from gill nets.

Predation tests

Four different types of predation tests were employed during the study.

In the first series, hand-made, wooden models of northern pike (14.5 cm length), trout-perch (7.0 cm), and spottail shiner (7.5 cm) were used to simulate prey. These models were suspended at middepth in the Study Stream directly in front of the observation tower. An event recorder, to which the models were connected, was mounted on a platform attached to the front of the observation tower. The event recorder used was designed by Moodie (1970) for recording predation on stickleback models. The models were connected to the recorder by a length of nylon line, so that any strike by northern pike would be recorded on pressure sensitive recording paper. Runs were conducted for 24 hour periods; a total of 398.75 hours recording were done with this system.

A second series of tests were carried out using a commercially produced immitation minnow (Rapala, Normark Co., Minneapolis) as a prey model. The model was 8.0 cm in length, and was constructed of balsa wood covered with plastic paint. The color was dark greenish-grey dorsally, grading to silver laterally, and white ventrally. In general appearance this model resembled a lake chub. The model was moved through the observation section on a nylon line, which was controlled from the observation tower. One traverse of the study section was considered to be one presentation; a total of 190 presentations of this model were made.

A third series of tests examined the importance of visual stimuli in releasing and directing a predatory attempt of northern pike. Live prey fish (trout-perch, spottail shiner, lake chub, and ninespine stickleback) were placed in water-filled glass vessels. These units were then suspended at middepth in the observation area for five minute periods. The reactions of the northern pike were then observed.

The fourth series of predation tests was used to examine the actual behavioral components of the predatory act of northern pike. Predatory acts were elicited by presenting single, live prey fish to northern pike in the observation area. The success and method of capture were recorded. Prey fish presented were of six species; longnose sucker, white sucker, trout-perch, lake chub, spottail shiner, and ninespine stickleback. A number of dead prey fish were also presented to northern pike during these tests, to determine if inert prey were acceptable.

Underwater observations

Scuba diving and snorkeling were employed to observe northern pike in the open littoral areas of Kakisa Lake and the Muskeg River. Information was also gathered on the presence of forage fish in the prime northern pike habitat. Observations carried out in this manner were used mainly to determine if activity of experimental fish was normal.

Transects

Transects, 30.5 m in length, were established on the lower Muskeg River (Figure 2). These ran parallel to shore, and included the whole band of emergent vegetation (average width approximately 8.0 m). Transects were traversed on foot, counting the number of northern pike present.

A second transect area was established on a narrow channel between two Scirpus beds in the littoral region off the mouth of the Muskeg River. These 22.0 m transects were traversed by boat. Counts of all northern pike in the channel were made, as well as estimates of numbers of all forage fish seen.

Both sets of transects were used to gain information on the relative abundance of northern pike and prey fish in the areas examined.

Statistical tests

The Chi-square test was used to analyse frequency data, with Yate's correction for continuity applied if any event had a frequency of less than five.

Model I Anova was applied to habitat use data, and significance of means was determined using Duncan's multiple range test.

Regression lines were calculated after the method of least squares (Sokal and Rohlf, 1969), with Bartlett's three-group method for Model II regression applied when both the dependant and independant variables were subject to error in measurement. Regression lines were compared using analysis of covariance (Snedecor and Cochran, 1967).

RESULTS AND DISCUSSION

I Limnology Results and Discussion

Limnological data were collected to allow a superficial comparison between the Study Stream, Muskeg River, and Kakisa Lake. The results of chemical analyses of water samples from these three areas are summarized in Appendix 3.

Levels of pH, phosphate, nitrate, and alkalinity were basically similar between the three areas, while the Study Stream was distinctly higher in total dissolved solids and $CaCO_3$ hardness. The dissolved oxygen levels tended to be lowest in the Study Stream, but the lowest values recorded there were above the critical level of 3.5 ppm (Toner and Lawler, 1969) for northern pike.

The limnology of Kakisa Lake and its tributary streams is examined in detail by Lamoureux (1973).

II Growth and Feeding

RESULTS

During the course of this study the northern pike population of Kakisa Lake was sampled at weekly intervals during the summer months. From these samples growth and feeding data were obtained.

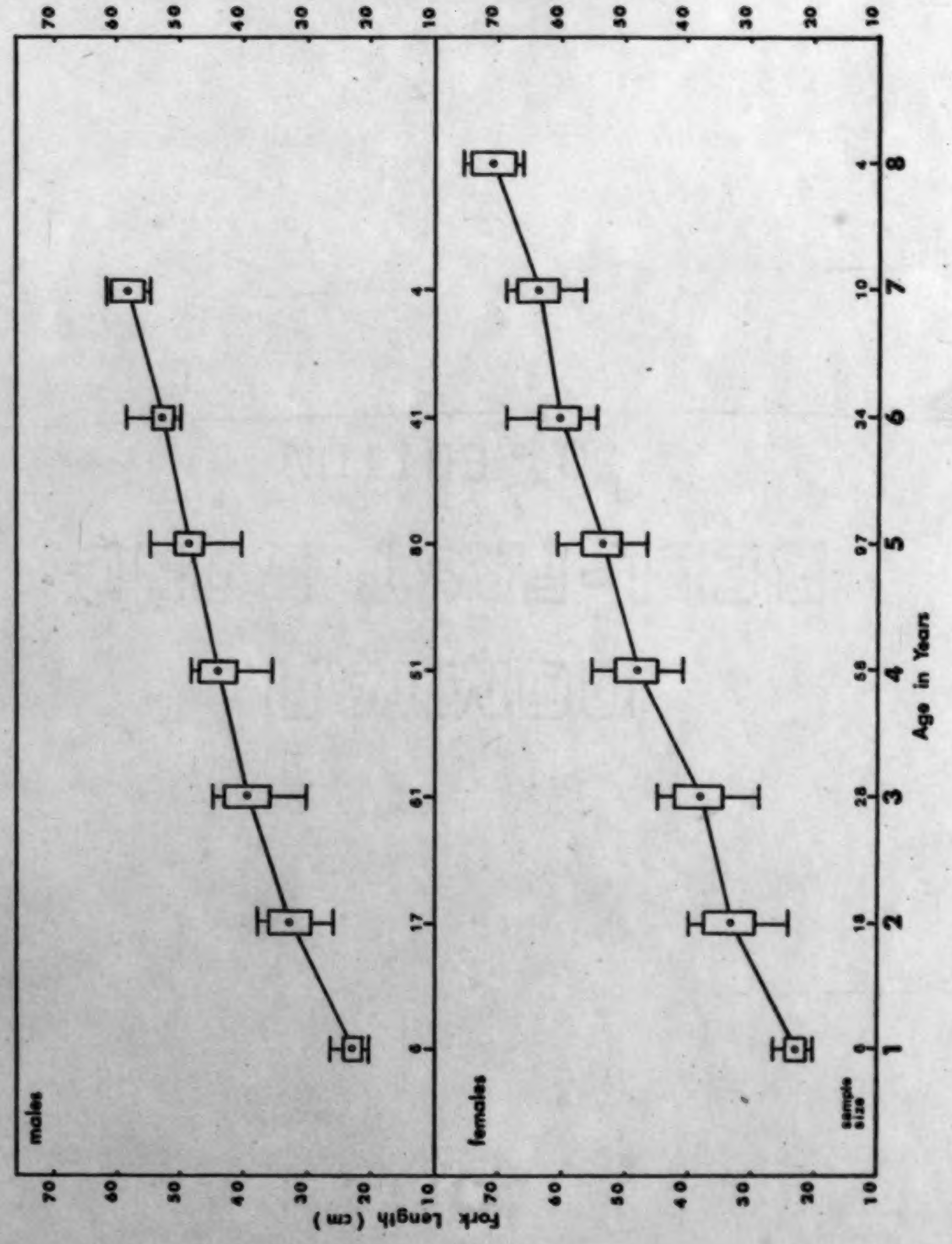
A. Growth

Mature northern pike examined exhibited a distinct sexual dimorphism in growth rates. For this reason the analysis of length-weight data have been conducted separately on each sex.

1. Length and Weight versus Age

The growth rates of male and female fish were similar for the first two years of life, but with the onset of maturation the growth rates began to diverge (Figure 5 and 6). Most males commenced spawning at the end of their third year of life, while most females first spawned at the end of their fourth year. From Figure 5 and 6 it is apparent that during their third year (age 2+) males showed a slightly higher growth rate than females of the same age. As a result, age 3+ males averaged 100 gm heavier than females of that age. However, the increase in growth rate of females

Figure 5. Average fork length of male and female northern pike at each age. Ranges and standard deviations indicated. Data from 1973 and 1974 combined. Sample size for each age class indicated on graph.


males
females
Fork Length (cm)
Age in Years
sample size
10
20
30
40
50
60
70
1
2
3
4
5
6
7
8
8
17
61
51
80
41
4
6
18
28
58
97
34
10
4

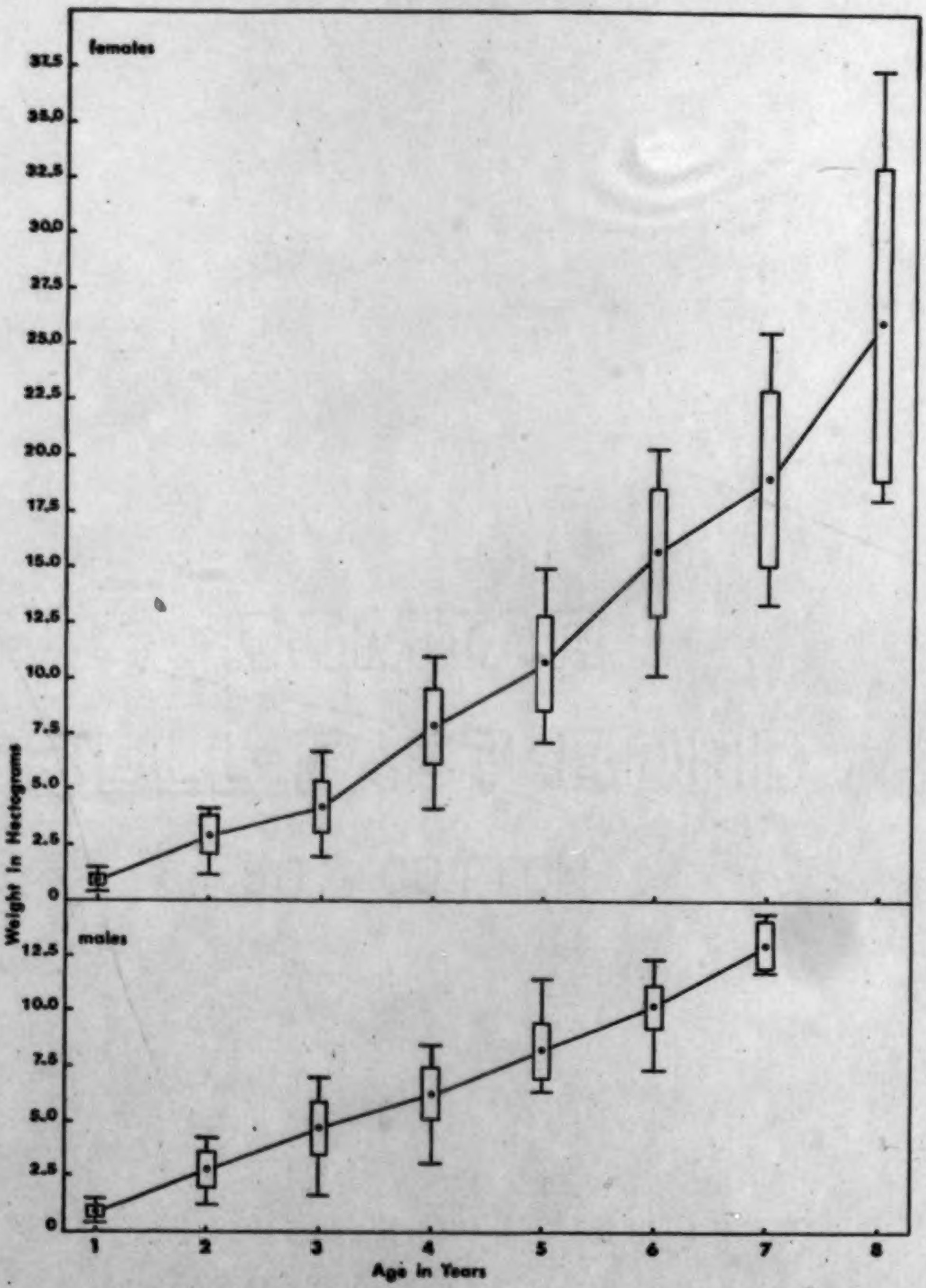


Figure 6. Average weight of age classes of male and female northern pike. Ranges and standard deviations indicated. Data from 1973 and 1974 combined. Sample sizes identical to those shown in Figure 5.

during their fourth year (3+) surpassed that previously shown by males. The result was that in all age classes from 4+ onward females tended to be larger than males. The data also indicate that females lived, on the average, one year longer than males in Kakisa Lake.

Ripe and spent individuals, and feeding and fasting individuals of both sexes were included in these data, this may partially account for the wider range of weights of females shown in Figure 6. However, Machniak (1975) states that large variation in size of individuals of the same age and sex is typical for this species.

Although mature females were faster growing than males, the relationship between length and weight was virtually identical for the two sexes (Figure 7). The difference between the slopes of the regression lines for males and females is not significant. The sample data deviate very little from the calculated regression lines (r^2= 0.96 males and 0.98 females).

2. Jaw Width

Lawrence (1957) and Johnson (1969) suggest that the the jaw width of piscivorous fish is critical in determining the size of forage fish which are consumed. Hence the jaw width measurement was made on northern pike examined.

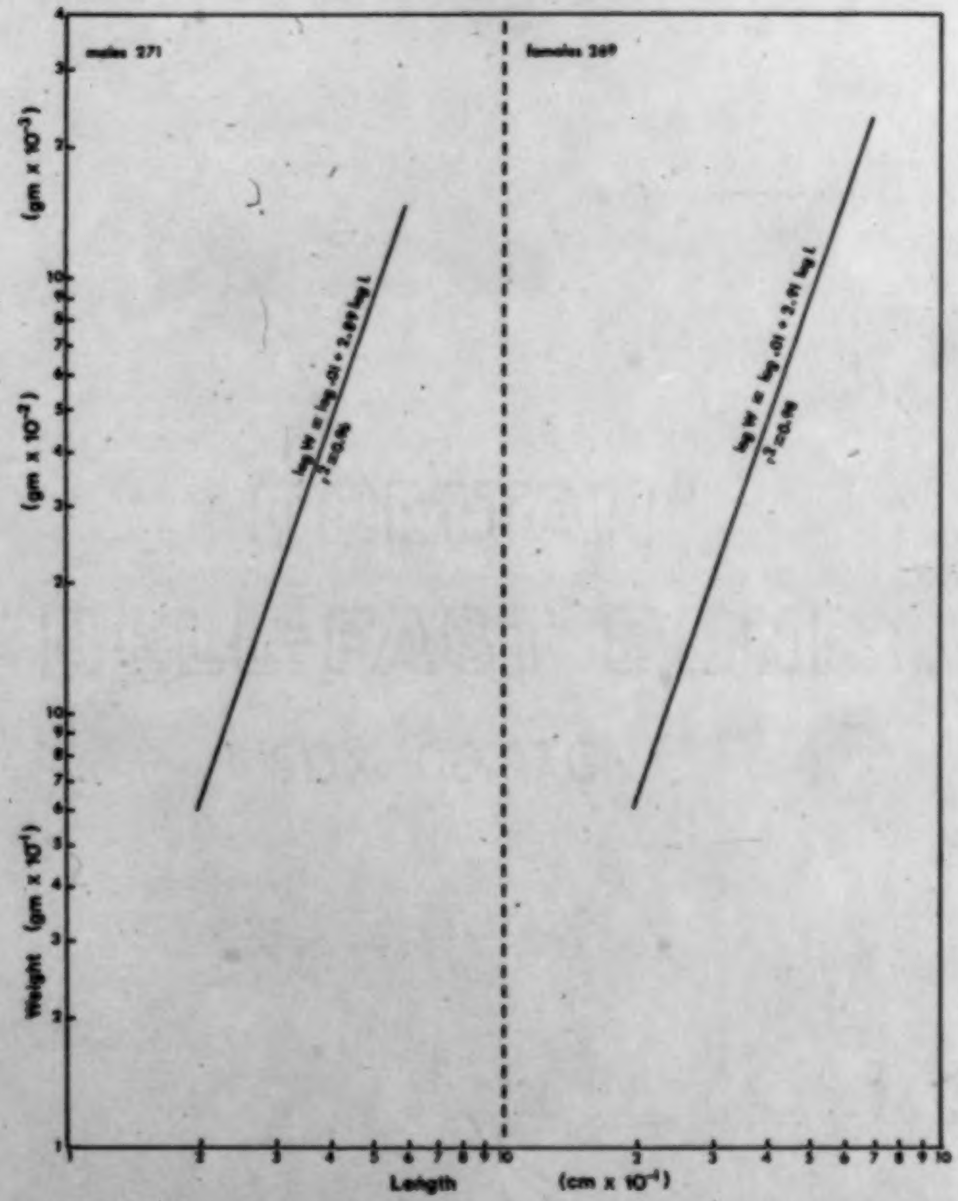


Figure 7. Length-weight regression of male and female northern pike. Data from 1973 and 1974 combined. Model II regression used (Sokal and Rohlf, 1969). Analysis of covariance indicates no significant difference between the slopes, intercepts, or elevations of the two lines. Sample sizes indicated.

Johnson (1969) reports wide variations in jaw widths of northern pike of the same fork length. However, plotting this relationship separately for males and females not only eliminates the wide variations, but also illustrates the existence of a sexual dimorphism in this character (Figure 8). The slopes of the regression lines are not significantly different, but the elevations are significantly different ($p<0.01$), which indicates that at any given fork length the average jaw width of females was greater than that of males. The data for each sex fit the respective regression line closely ($r^2= 0.92$ males and 0.95 females). The magnitude of the difference between jaw widths of males and females increased gradually with growth of the fish (Figure 8).

B. Feeding

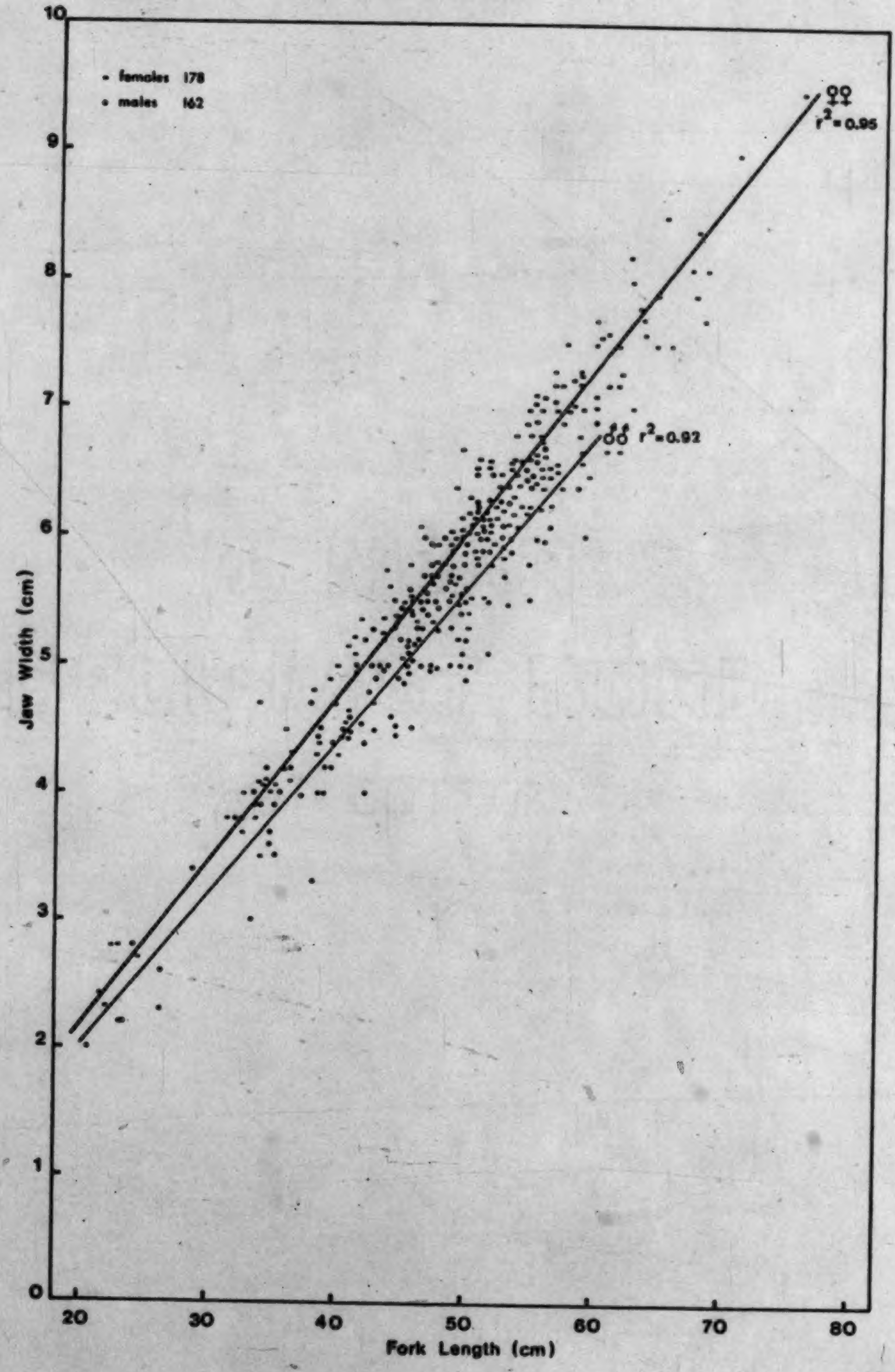
Food habits of gillnetted northern pike were examined over the two summers, with the total sample comprising 641 individuals between 20 and 75 cm fork length. The data thus represent feeding during the spawning and post-spawning periods by mature fish. Over the course of the summer period shifts in the frequency of feeding were apparent, together with temporal changes in the portions and amounts of the total prey spectrum utilized. The data provide some indirect indications of the importance of prey size, prey

Figure 8. Fork length-jaw width regression of male and female northern pike. Data from 1974. Model II regression used. Analysis of covariance indicates slopes and intercepts of lines not significantly different ($p>0.05$), elevations are significantly different ($p<0.01$).

Regression Equations

Females - Jaw Width = -0.43 + 0.13 Length

Males - Jaw Width = -0.39 + 0.12 Length


• females 178
• males 162
♀♀ r^2 = 0.95
♂♂ r^2 = 0.92
Jaw Width (cm)
0
1
2
3
4
5
6
7
8
9
10
Fork Length (cm)
20
30
40
50
60
70
80

availability, and prey behavior in determining the food habits of northern pike.

1. General Food Intake Patterns

Feeding by northern pike was lowest during May, at the time of spawning, as indicated by the high percentage of fish having empty stomachs at this time (Table 1 and Figure 9). This finding is in agreement with that of Frost (1954) who reports the occurrence of a spawning fast in northern pike from Windermere. Invertebrates were the exclusive food of 25% of the northern pike captured at this time. The numbers of invertebrates eaten per fish were low during May ($\bar{x}$ = 14 organisms), with 50% of the fish that fed on invertebrates containing only one or two individuals. The low percentage of northern pike containing fish at this time indicated that active feeding was at a low level in the spawning population. Further support for this idea is gained from the fact that prey fish were almost totally digested when northern pike were captured moving into the spawning areas. These prey must have been consumed a number of days prior to capture of the predator, since digestion of fish requires approximately three to five days at water temperatures of one to ten degrees Celsius (Popova, 1967).

With termination of spawning and return to the lake area in June, the frequency of occurrence of empty stomachs

Month	Contents of Stomach Empty	 Invertebrates Only	 Fish	Totals
May	129 69%	51 25%	24 12%	204
June	58 36%	38 24%	65 40%	161
July	64 43%	20 13%	65 44%	149
August	47 37%	2 2%	78 61%	127
Totals	298	111	232	641

Table 1. General food habits of northern pike in Kakisa Lake, data from 1973 and 1974 combined. Values given as numbers of fish (and percent of sample each month) containing food items indicated.

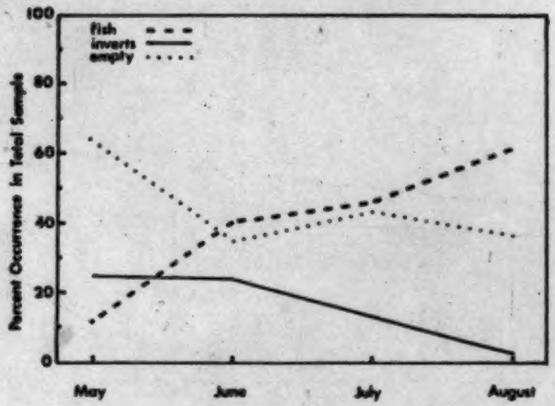


Figure 9. General food habits of northern pike in Kakisa Lake, data from 1973 and 1974. Values given as percent occurrence of each food item in total sample each month. Abbreviation: inverts = invertebrates.

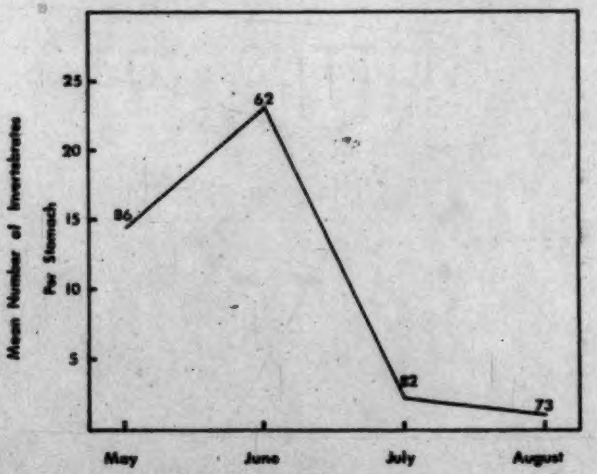


Figure 10. Mean number of invertebrates in stomachs of northern pike which contained invertebrates each month, data from 1973 and 1974 combined. Numbers on graph indicate percent of fish containing fewer than the mean number of invertebrates for that month.

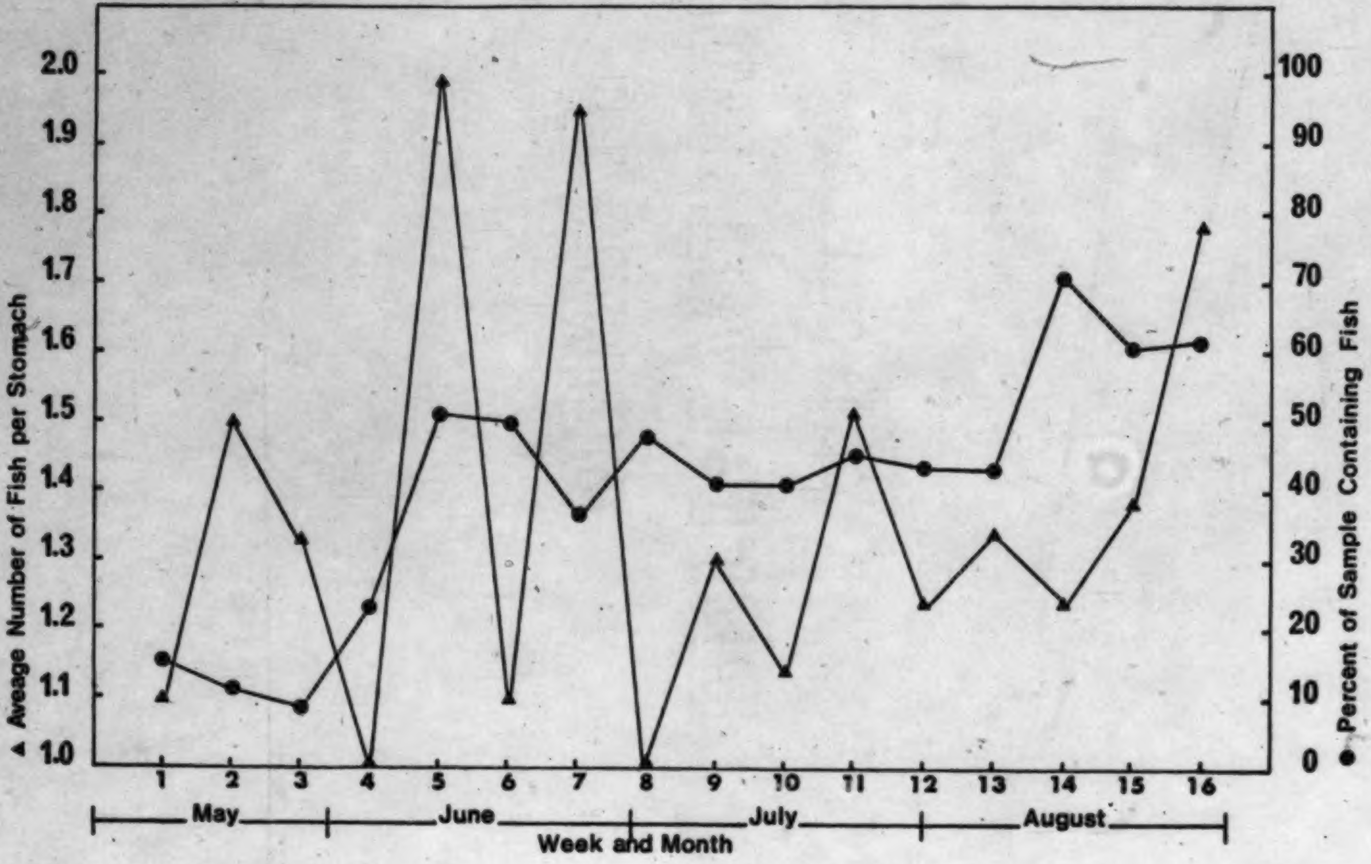
declined (Figure 9). Day to day fluctuations in feeding occurred, but for the remaining summer months the average percent occurrence of empty stomachs remained near 35 to 40%.

The proportion of the population feeding on invertebrates was the same in June (24%) as in May. Numbers of invertebrates consumed by fish rose to an average of 24 per stomach in June (Figure 10). At this time only 63% of the stomachs of invertebrate feeding fish contained less than the average number of organisms. The proportion of the northern pike population feeding on fish rose in June to almost four times the level observed in May (Figure 9). The average number of prey fish consumed fluctuated from week to week during the resumption of active feeding in June (Figure 11). Through the mid to late summer period of July and August feeding on invertebrates steadily declined to almost insignificant levels (Figure 9 and 10). The percent of the population exhibiting piscivorous habits increased gradually through July and early August, and then rose more sharply to a level of 60 to 70% in mid to late August (Figure 11).

2. Food Species

The importance of the various prey items in the summer diet of northern pike was calculated from percent occurrence of a species times the average amount (gm) of that species consumed by individual northern pike. These data are based

Figure 11. Piscivorous habits of northern pike over the summer, on a week by week basis. Data from 1973 and 1974 combined. Average number of fish per stomach calculated from only those predators containing fish. Percent of sample containing fish calculated from total sample each week.



on only those fish which were feeding. The relative contributions of the various food items to the diet of northern pike, in many cases, were different in the two years of the study (Figure 12). Areas within each rectangle indicate the relative importance of the item specified. It is evident that fish formed the most significant component of the total diet. However, a relatively unique feature of the diet of Kakisa Lake northern pike did emerge. The generally high percent occurrence of invertebrates in the diet could at times result in their importance being greater than some of the smaller forage fish species. This type of situation has been reported by few workers, Munro (1957) being one. The species and numbers of invertebrates consumed by northern pike are shown in Appendix 4.

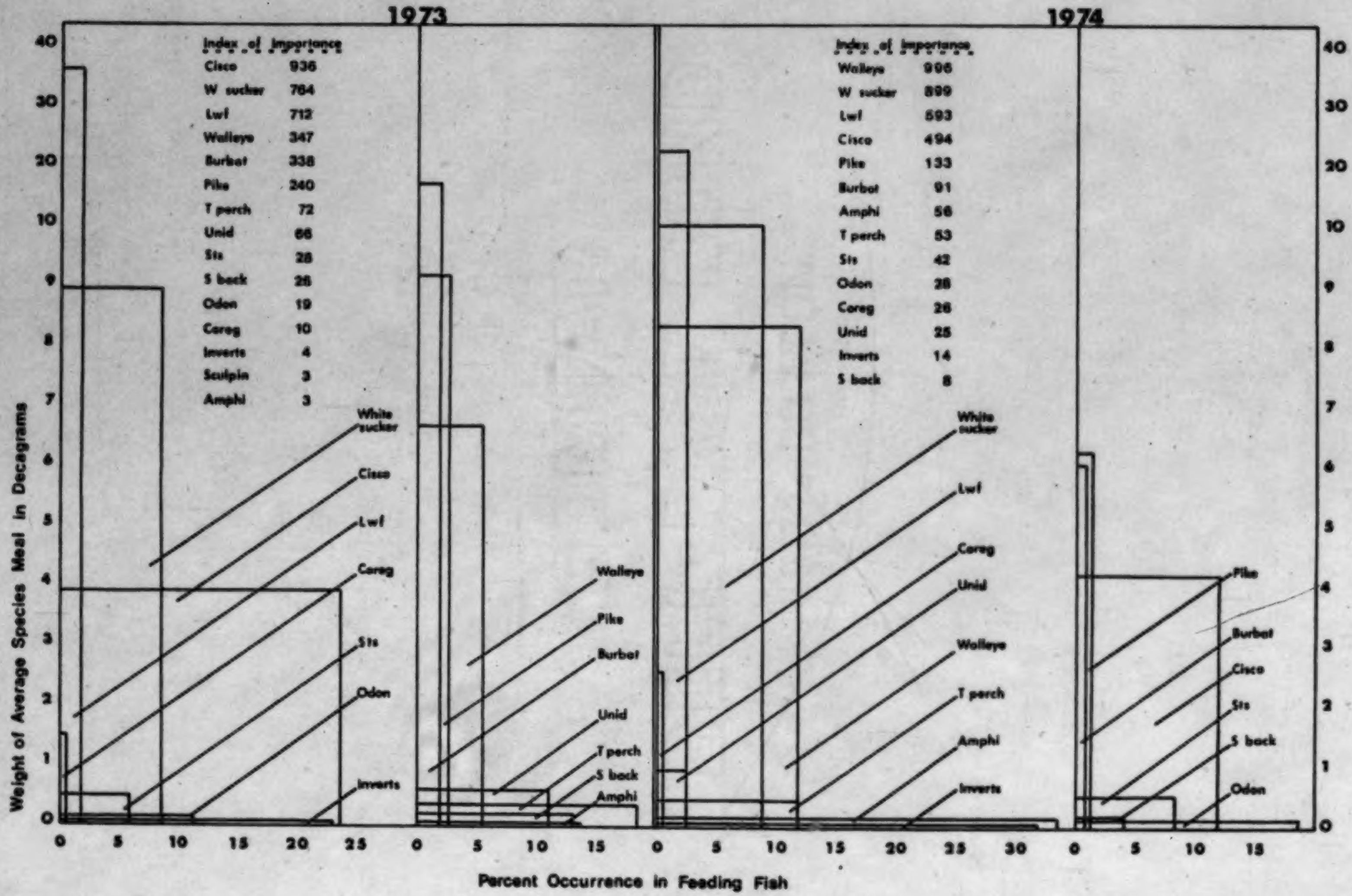
The six major food fish were cisco, walleye, white sucker, lake whitefish, burbot, and northern pike. It appeared that the relative positions of importance of these major species could change from year to year (Figure 12). Ivanova (1969) reports similar shifts in the diet composition of northern pike from the Rybinsk Reservoir.

In 1973 cisco were the most important prey species in the summer diet, while in 1974 walleye occupied this position (Figure 12). White suckers and lake whitefish occupied second and third positions of importance respectively in both years. For these latter two species, frequencies of

Figure 12. Importance of the prey items in the diet of northern pike during the period May through August, 1973 and 1974. Index of Importance values calculated from areas under each species rectangle: weight of average species meal times percent occurrence of species in stomachs of feeding northern pike.

Abbreviations

W sucker	- White sucker	S back	- Ninespine stickleback
Lwf	- Lake whitefish	Odon	- Odonata
Pike	- Northern pike	Coreg	- Unidentified coregonids
T perch	- Trout-perch	Inverts	- Other invertebrates
Unid	- Unidentified fish	Sculpin	- Slimy sculpin
Sts	- Spottail shiner	Amphi	- Amphipoda


1973
1974
Index of Importance
Cisco 936
W sucker 764
Lwf 712
Walleye 347
Burbot 338
Pike 240
T perch 72
Unid 66
Sts 28
S back 26
Odon 19
Coreg 10
Inverts 4
Sculpin 3
Amphi 3
Index of Importance
Walleye 996
W sucker 899
Lwf 593
Cisco 494
Pike 133
Burbot 91
Amphi 56
T perch 53
Sts 42
Odon 28
Coreg 26
Unid 25
Inverts 14
S back 8
White sucker
Cisco
Lwf
Coreg
Sts
Odon
Inverts
Walleye
Pike
Burbot
Unid
T perch
S back
Amphi
White sucker
Lwf
Coreg
Unid
Walleye
T perch
Amphi
Inverts
Pike
Burbot
Cisco
Sts
S back
Odon
Weight of Average Species Meal in Decagrams
0
1
2
3
4
5
6
7
8
9
10
20
30
40
Percent Occurrence in Feeding Fish
0
5
10
15
20
25
30

occurrence in northern pike stomachs were low, but the average size of the species meal was large resulting in a significant contribution to the total diet. Walleye were the fourth most important food species in 1973, while in 1974 cisco occupied this position. Burbot and northern pike occupied positions five and six respectively in 1973, and positions six and five respectively in 1974. The three smaller forage fish species - trout-perch, spottail shiner, and ninespine stickleback - occupied positions seven, nine, and ten respectively in 1973, and positions eight, nine, and fourteen in 1974. Of the other two small forage fish present in the lake, slimy sculpin occurred in only one stomach, and lake chub were never identified from northern pike stomachs. Unidentified fish and unidentified coregonids changed from positions eight and twelve respectively in 1973 to positions twelve and eleven respectively in 1974. This slight drop was mainly due to increased accuracy of stomach contents identification in the second year of the study. During 1973 the general importance of invertebrates was low, with odonatans in position eleven, other invertebrates in position thirteen, and amphipods in position fifteen. In 1974 invertebrate consumption increased sharply, such that amphipods rose to seventh position and odonatans rose to tenth position.

3. Seasonal Changes in Diet

The food habits of northern pike underwent transitions during the spring to fall period. In Kakisa Lake four separate feeding periods occurred over the summer, and these roughly corresponded to the four months May, June, July, and August. These periods were:

1. The spring spawning fast.
2. Spring to early summer post-spawning period, with resumption of active feeding.
3. Mid to late summer period of stable water temperatures and general feeding.
4. Late summer to fall period of unstable weather conditions, temperature decline, and heavy feeding.

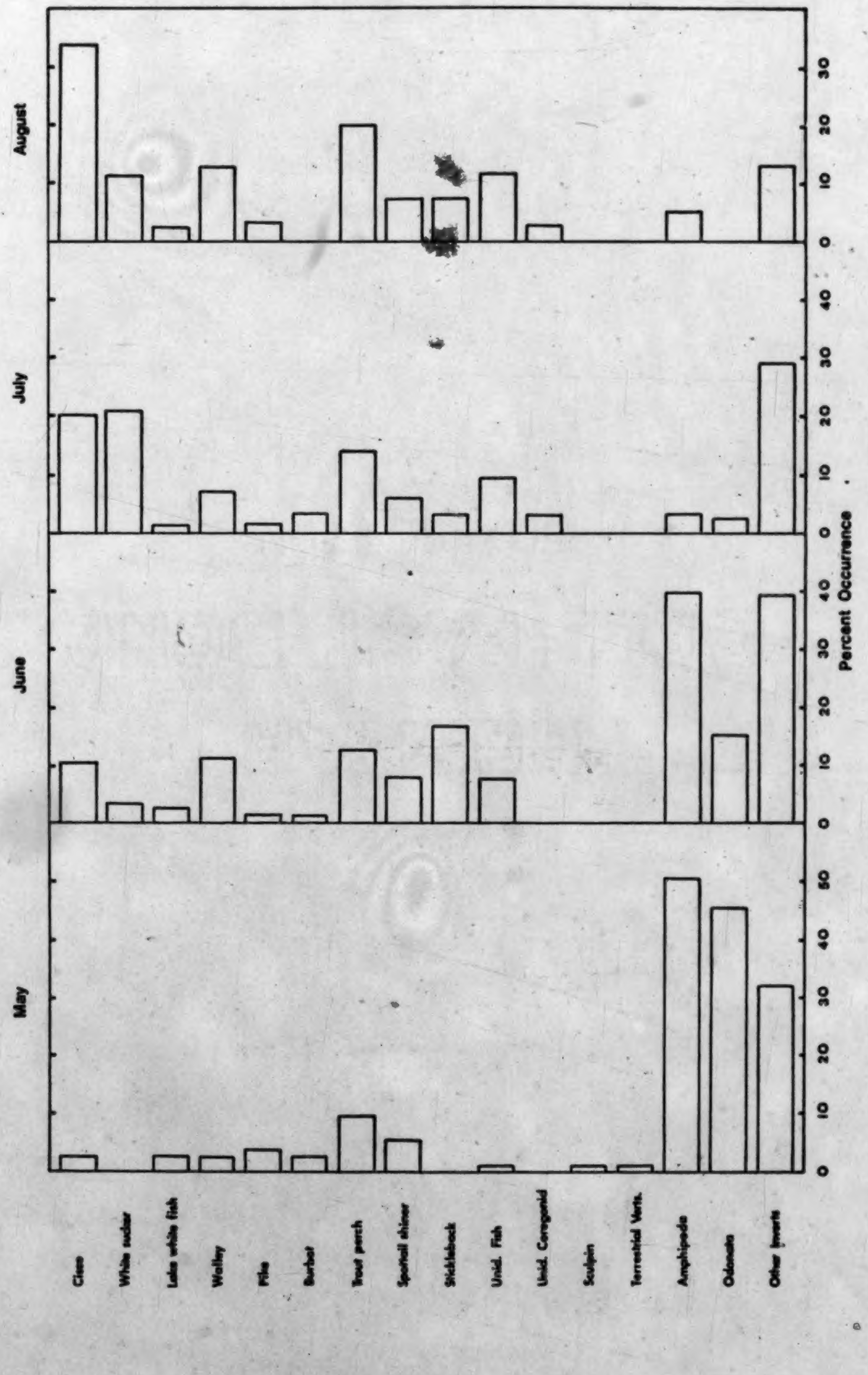
The seasonal food habits of northern pike are expressed as percent occurrence of food items in feeding fish (Table 2 and Figure 13).

Cisco were seldom consumed by northern pike during May. The percent occurrence then rose gradually through the remaining summer months. In August, cisco occurred in 34% of the feeding northern pike, which represented the highest level attained by any prey-fish species during the summer. White suckers followed a pattern of occurrence similar to that of cisco up to the month of July. Then in August their frequency of occurrence dropped to half the level of July. Lake whitefish had a stable but low level of occurrence, of

Table 2. Seasonal changes in the diet of northern pike over the summers of 1973 and 1974. Values in percent occurrence of food items in feeding fish.

Food Item	May	June	July	August
Cisco	2.7	10.6	20.0	33.8
White sucker	0.0	3.9	21.2	11.3
Lake whitefish	2.7	2.9	1.2	2.5
Walleye	2.7	11.7	7.1	12.5
Northern pike	4.0	1.9	1.2	3.8
Burbot	2.7	1.0	3.5	0.0
Trout-perch	9.3	12.6	14.1	20.0
Spottail shiner	5.3	7.8	5.9	7.5
Sticklebacks	0.0	16.5	3.5	7.5
Unid. fish	1.3	7.8	9.4	11.3
Unid. coregonid	0.0	0.0	3.5	2.5
Sculpin	1.3	0.0	0.0	0.0
Terrestrial vertebrate	1.3	0.0	0.0	0.0
Amphipoda	50.7	39.8	3.5	5.0
Odonata	45.3	15.5	2.4	0.0
Other invertebrates	32.0	38.8	29.4	12.5

Figure 13. Percent occurrence of food items in feeding northern pike each month. Data from 1973 and 1974 combined.


May
June
July
August
Cisco
White sucker
Lake white fish
Walley
Pike
Burbot
Trout perch
Spottail shiner
Stickleback
Unid. Fish
Unid. Coregonid
Sculpin
Terrestrial Verts.
Amphipoda
Odonata
Other Inverts
0
10
20
30
40
50
Percent Occurrence

2%, over all four months. Walleye, like most other species, occurred least frequently in northern pike stomachs during May. For the rest of the summer the frequency of occurrence of walleye fluctuated around the 10% level. Cannibalism by northern pike was highest in May and August, although the percent occurrence never exceeded 4%. Burbot remained very low in frequency of occurrence for the first three months of the summer, and were absent from the diet in August. Trout-perch, while at their lowest frequency of occurrence in May, were the most frequently consumed fish that month. Their occurrence rose through the summer, similar to that of cisco, and reached a peak of 20% in August. Spottail shiners showed a stable frequency of occurrence near 7% for the entire four month period. Nine-spine sticklebacks had a unique pattern of occurrence for a fish species. They were absent from the diet in May, but abruptly rose to their highest level of 17% in June. Their occurrence then declined to 3% in July, and showed a slight rise again in August. Sculpins and terrestrial vertebrates seemed to be only incidental in the diet.

The frequency of occurrence of invertebrates, in general, was opposite to that seen for fish. Amphipods and odonatan nymphs reached their highest levels of occurrence in May. In June amphipods dropped slightly to 40% occurrence in northern pike stomachs, while odonatans fell to less than one-half the May level. By July both groups declined to only 3% frequency of occurrence. In August amphipods rose very slightly, and odonatans were absent from the diet, a condition apparently related to changes in the population size of these organisms. Other invertebrates (Table 2) were consumed by 30% of the feeding predators in May. In June the consumption of this group increased by a quarter, and thereafter declined gradually to a low of 13% in August.

Generally, predators exhibited low levels of piscivorous habits during the spring, but frequently consumed invertebrates. As the summer progressed consumption of forage fish rose, while invertebrate consumption declined.

4. Predator Size and Diet Composition

Data obtained indicate that the prey species composition of the diet changed with increase in size of northern pike. The diets of five fork length size classes of adult northern pike were examined (Table 3).

Cisco first appeared at low levels in the diet of 30-39 cm predators, and rose to the highest occurrence in the 50-59 cm predator size class. White suckers followed a pattern similar to that of cisco, except that white suckers were at high frequencies of occurrence in northern pike of 50-59 and also 60-69 cm fork length. Lake whitefish occurred most frequently in the 60-69 cm size class of predator, and were not consumed by northern pike of less

Table 3. Percent occurrence of the various prey items in the diet of five size classes of northern pike. Size classes based on fork length in cm. Data from 1973 and 1974 combined, as percent occurrence in feeding fish.

Food Item	Fork Length Class 20-29	 30-39	 40-49	 50-59	 60-69
Cisco	0.0	6.5	17.9	24.8	10.0
White sucker	0.0	3.2	6.3	15.2	15.0
Lake whitefish	0.0	0.0	0.0	4.0	15.0
Walleye	9.0	1.6	4.5	13.6	15.0
Burbot	0.0	0.0	1.8	1.6	10.0
Northern pike	4.5	0.0	4.5	1.6	5.0
Trout-perch	40.9	37.1	8.9	9.6	5.0
Spottail shiner	13.6	6.5	8.0	6.4	5.0
Stickleback	27.3	16.1	4.5	4.0	5.0
Unid. fish	0.0	9.7	6.3	9.6	0.0
Unid. coregonid	0.0	0.0	1.8	2.4	0.0
Invertebrates	45.5	59.7	52.7	32.0	25.0
% of sample feeding	84.6	43.1	35.1	48.3	50.0
Sample size	26	82	235	258	40

than 50 cm fork length. Walleye were consumed by all size classes of northern pike. The young of the year walleye occurred in the diet of 20-29 cm northern pike. Intermediate sized northern pike, 30-49 cm fork length, took few walleye, but this prey became gradually more important in the diet of predators in the 50-59 cm and 60-69 cm size classes. Burbot were absent from the diet of northern pike below 40 cm fork length, and attained a maximum level of occurrence in predators of 60-69 cm. Cannibalism occurred in all but the 30-39 cm size class of northern pike, but tended to be low in all cases. The three small forage fish species all followed a similar pattern of maximum occurrence in northern pike of 20-29 cm, and correspondingly diminished in frequency of occurrence in each successively larger size class of predator. Of these three species, trout-perch occurred most frequently in northern pike stomachs overall, with ninespine sticklebacks second, and spottail shiners third. Invertebrates occurred most frequently in northern pike of 30-39 cm fork length, and showed a gradual decline in each successively larger size class of predator.

5. Predator-prey Size Relationships

Data indicate that size selection of prey is exercised by northern pike, which may help to explain the differences in the composition of the diets of the various size classes of northern pike.

The ratio of prey length to predator length has been used by Frost (1954) and Lawler (1965) to examine the importance of predator-prey size relationships. Present findings indicate no significant correlation between predator length and the ratio of prey length to predator length when all size classes of predator were grouped for the analysis (Table 4). This was clearly a result of a negative correlation between these two parameters in the smallest through to the intermediate (40-45 cm) size classes of predator (Table 4). The correlation then became positive in the intermediate (45-50 cm) through to the largest size classes of predator (Table 4). This indicates the occurrence of a distinct change in the food habits of northern pike once they surpass 45 cm in fork length. These findings also suggest that length of prey may not be the most critical measurement determining the maximum size of prey consumed.

Most prey fish are turned on their side before being ingested by northern pike. This suggests that the critical relationship, determining maximum size of prey consumed, is that between the maximum jaw width of the predator and maximum body depth of prey fish. Johnson (1969) suggests, but does not statistically test, the importance of this relationship. Present findings indicate that the correlation between the jaw width of northern pike and the ratio of prey depth to predator jaw width is significant ($r = +0.91$) (Table 5).

Table 4. The relationship between predator length and the average prey length to predator length ratio. Data from 1973 and 1974 combined.

Fork length of northern pike in cm	20 to 25	25 to 30	30 to 35	35 to 40	40 to 45	45 to 50	50 to 55	55 to 60	60 to 65	65 to 75
Average prey length to predator length ratio	.30	.22	.20	.18	.18	.26	.29	.28	.36	.38

r = +0.69

Overall average prey length to predator length ratio = 0.27

Table 5. The relationship between jaw width of predator and the average maximum body depth of prey to jaw width of predator ratio. All measurements in cm. Data from 1973 and 1974 combined.

Jaw width northern pike	3.5 to 4.0	4.0 to 4.5	4.5 to 5.0	5.0 to 5.5	5.5 to 6.0	6.0 to 6.5	6.5 to 7.0	7.0 to 7.5	7.5 to 8.0	8.0 to 8.5	8.5 to 9.0	9.0 to 9.5	9.5 to 10
prey depth to predator jaw width ratio	.35	.37	.34	.39	.44	.46	.48	.43	.50	.50	.62	.73	.73

r = +0.91

Overall prey depth to predator jaw width ratio = 0.49

It was shown that female northern pike, on the average, had wider jaws than males of the same fork length (Figure 8). It might be expected that this dimorphism could, to some extent, effect the relative sizes of prey fish consumed by each sex.

As expected, especially in the larger size classes of northern pike, females tended to consume prey fish of greater body depth than those consumed by males of the same fork length (Figure 14). The slopes of the regression lines are significantly different ($p<0.01$). The r^2 values are low, but given the opportunistic nature of northern pike predation this might be expected in the wild.

The prey size differences between male and female northern pike were manifest in the species composition of the diet of each sex. Females tended to utilize the larger species of prey fish to a greater extent than did the males (Table 6). Most evident was the complete absence of lake whitefish (deepest bodied prey fish) from the diet of male northern pike, and the 5.4% frequency of occurrence of this species in the diet of females. White suckers also had a disproportionately higher percent occurrence in the diet of female northern pike (Table 6). Cisco, walleye, burbot, and northern pike all had a slightly higher frequency of occurrence in female northern pike stomachs. Smaller forage fish, occurred more frequently in the diet of males (Table 6).

Figure 14. Regression analysis of the relationship between fork length of male and female northern pike and the maximum body depth of prey fish consumed. Model II regression used. Analysis of covariance indicates mean squares of deviations not significantly different between lines ($p>0.40$), slopes are significantly different ($p<0.001$).

Regression Equations

Females - Prey Depth = -2.90 + 0.12 Predator Length

Males - Prey Depth = -0.94 + 0.07 Predator Length

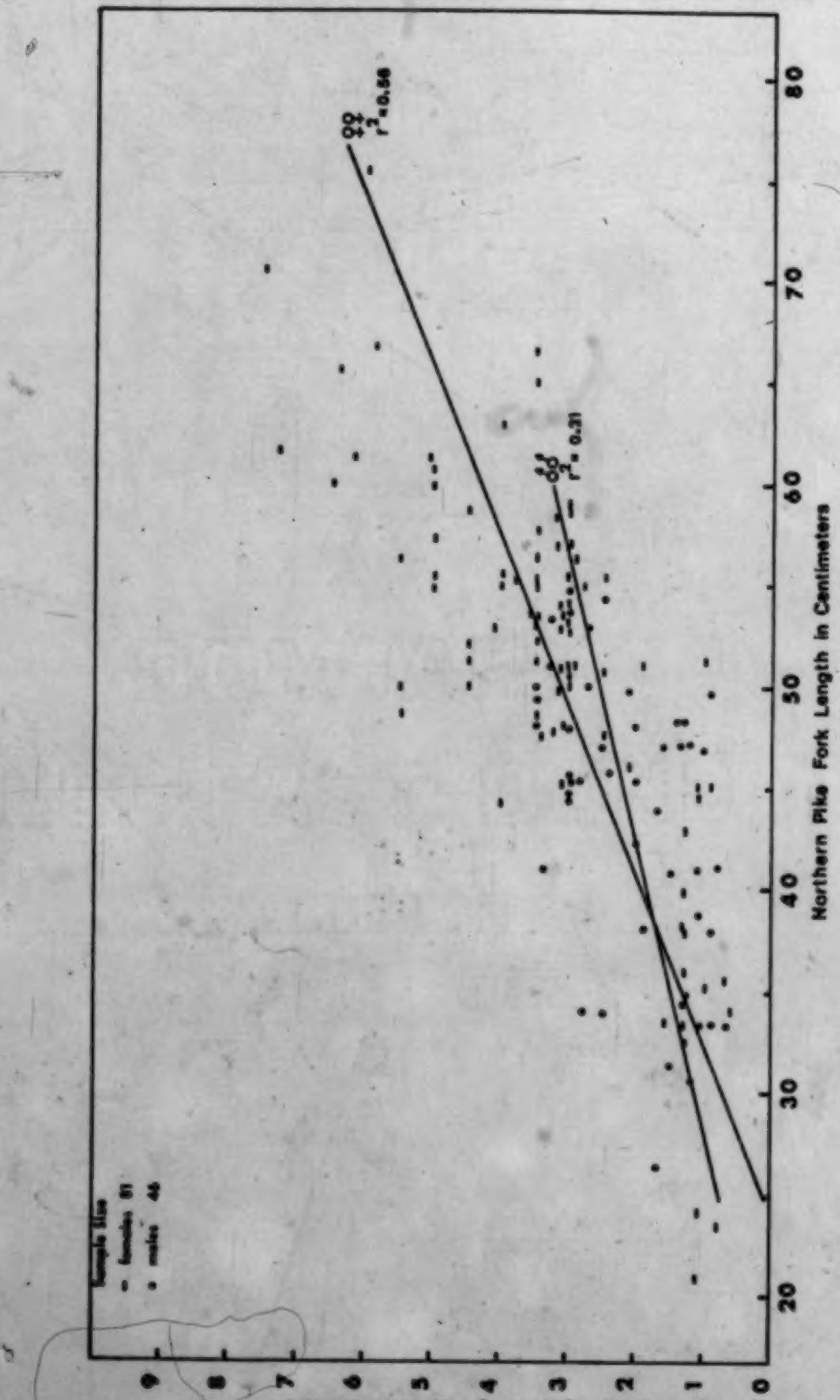

Maximum Body Depth of Prey Fish in Centimeters
0
1
2
3
4
5
6
7
8
9
Northern Pike Fork Length in Centimeters
20
30
40
50
60
70
80
Sample Size
– females 81
• males 44
♀♀ r^2=0.56
♂♂ r^2= 0.31

Table 6. The average percent occurrence of the major food items in the diet of male and female northern pike from Kakisa Lake. Data from 1973 and 1974 combined. Values given as percent occurrence of food items in feeding fish.

Food Item	Percent Occurrence in	
	Males	Females
Cisco	18.5	20.5
White sucker	5.6	12.7
Lake whitefish	0.0	5.4
Walleye	10.5	10.6
Burbot	1.9	2.1
Northern pike	2.2	3.8
Trout-perch	13.4	14.6
Spottail shiner	6.3	5.7
Stickleback	11.6	4.4

DISCUSSION

A. Growth

The growth rates of northern pike from Kakisa Lake appear to be considerably higher than those reported by Miller and Kennedy (1948) for Great Slave Lake fish. The rates of growth in the Kakisa Lake population, never the less, are lower than those found at more southerly latitudes, such as Seibert Lake, Alberta (Makowecki, 1973). Due to its shallow basin Kakisa Lake has a relatively long ice free period, and exhibits higher average summer water temperatures than is usual for lakes at this latitude. These two limnological factors may largely explain why the growth rate of Kakisa Lake northern pike is higher than that of Great Slave Lake fish.

Miller and Kennedy (1948) also state that females live longer than males, but that males and females of the same age are similar in size. In Kakisa Lake females do tend to live one year longer than males, but the growth rate of mature females exceeds that of males of the same age (Figure 5 and 6). In this respect Kakisa Lake northern pike resemble more southerly populations, such as those studied by Solman (1945) and Clark and Brown (1965). In those populations females tend to display higher growth rates than males. Healy's (1956) work is supported by present findings, since he finds that the growth rates of males and females do not differ significantly before sexual maturity. Frost and Kipling (1959), and Clark and Brown (1965) report mature females to be heavier than mature males of the same length. This is not expressed in the Kakisa Lake population, where mature individuals of the two sexes display similarity of weight at any given length (Figure 7). The closeness of the regression lines (Figure 7) indicates that in Kakisa Lake male and female northern pike are alike in general body form.

The maximum ages of seven and eight years for male and female northern pike respectively are extremely low (Figure 6). For males and females respectively, Miller and Kennedy (1948) list 14 and 17 years as maximum age in Great Slave Lake, and Makowecki (1973) lists 14 and 13 years as maximum age in Seibert Lake. Scott and Crossman (1973) state that northern pike display "a decline in growth rate northward and a corresponding increase in longevity". Thus it might be expected that Kakisa Lake fish would have a shorter life span than the slower growing Great Slave Lake population, but a longer life span than the faster growing Seibert Lake northern pike. This abnormity appears to be a direct result of the selective removal of most large northern pike by the intensive commercial fishery operating on Kakisa Lake during the spring spawning run.

B. Feeding

1. Food Intake Patterns

The spawning fast exhibited by Kakisa Lake northern pike is consistent with the findings of McNamara (1937) and Frost (1954), but not with the suggestions of Healy (1956) that no such fast exists. It seems that such a reduction in feeding, especially piscivorous, might have a definite value to northern pike. Because of the sexual dimorphism in body size, many males involved in spawning activities are within the acceptable prey size range of older females. From observations made it is evident that under normal feeding conditions northern pike will resort to cannibalism if the opportunity is available. Normal predatory responses during the spawning run could result in a significant diminution of the ranks of smaller males and females. Cannibalistic acts would also have a disruptive effect on actual spawning activities. A reduction in feeding might also insure that spawning occurred rapidly, under optimal conditions. With post-spawning return to the lake, feeding resumes, and cannibalism reaches its highest level of the summer; which is apparently a result of the temporarily high densities of post-spawning individuals dispersing from the spawning streams. This hypothesis may also partially explain observations that male northern pike enter the spawning grounds seven to ten days prior to females, and leave one to three weeks after females. With this strategy males could, to some extent, avoid the concentrations of potential predators both before and after spawning.

The pattern of consumption of invertebrates (Figure 10) during the spring and early summer period suggests that the spawning fast is not merely a result of low food availability. During May the late instars of zygopterans, anizopterans, and amphipods are at their peak abundance and availability in the littoral areas and spawning rivers of Kakisa Lake (Lamoureux, 1973; D. Musbach, pers. comm. 1976). Although 25% of the northern pike captured in May did contain invertebrates as exclusive food, over 50% of these fish had only one or two individuals in their stomach. This suggests that feeding on these abundant organisms is curtailed at this time, since following spawning the number of invertebrates per stomach increases sharply (Figure 10).

Popova (1967) and Roberts (1975) indicate the importance of considering rate of digestion when using percent occurrence of empty stomachs as an indicator of feeding rate in a population of piscivorous fish. In May, when water temperatures are low, the percent occurrence of empty stomachs in Kakisa Lake northern pike is 65%. At May water temperatures, digestion of prey can require from three to five days (Popova, 1967). Thus a predator is only required to feed every three to five days to have food in its stomach continually. In June, July, and August the occurrence of empty stomachs remained near 40% (Figure 9). At summer water temperatures, digestion requires only one to two days (Popova, 1967). Thus a fish must feed at least every second day to have food in its stomach continually. As a result of this difference, the spring feeding rates are actually overestimates when compared to the summer and early fall rates. It appears that feeding rates in the spring may actually be 20 to 25% lower than those predicted from simple occurrence of empty stomachs in the population. This fact may suggest one reason for the failure of other studies to detect a spring spawning fast in northern pike populations.

The wide week to week fluctuations in feeding intensity, (numbers of fish per stomach) illustrated in Figure 11, are a salient feature of northern pike populations. Frost (1954) and Ince and Thorpe (1976) agree that the species is particularly well adapted for surviving extended periods of starvation. Frost (1954) also states, "that it is a popular belief that periodic abstinence characterizes northern pike feeding habits." Roberts (1975) suggests the existence of a lag period between completion of digestion of food and consumption of the next meal. These findings are similar to those of the present study, and may explain the characteristically high incidence of empty stomachs in northern pike populations at all times of the year.

2. Food Species

The tendency of Kakisa Lake northern pike to be mainly piscivorous parallels the findings of Frost (1954), Healy (1956), Seaburg and Moyle (1964), and others. In contrast to most studies, the percent occurrence and relative importance of invertebrates in the diet is higher than that reported for more southerly populations. In the Murphy Flowage, Wisconsin, the maximum percent occurrence of invertebrates in the diet of northern pike was 2.7% (Johnson, 1969). Toner and Lawler (1969) report a 3.6% occurrence of insects in Minnesota fish. In Kakisa Lake it appears that the large invertebrates resident in and around the mouths of the spawning rivers are the first abundant food source encountered by post-spawning northern pike. Scuba diving observations suggest that forage fish are not abundant in the spawning rivers when northern pike are returning to the lake. These facts may account for the abnormally high incidence of invertebrates in the diet of Kakisa Lake fish during late May and early June (Figure 12).

Year to year fluctuations in the importance of various prey species in the diet of northern pike (Figure 12) have also been reported by Frost (1954), Lawler (1965), Johnson (1969), and Ivanova (1969). Ivanova (1969) suggests that such changes are due to fluctuations in prey availability, caused by factors such as altered water levels, which affect prey spawning and feeding habits. Basic differences in the year class strengths of prey species have also been implicated in this respect (Lawler, 1965).

The two coregonid species are abundant in the pelagic regions of Kakisa Lake. Shoreward feeding and spawning movements result in concentrations of these fish in areas frequented by northern pike. Relative numbers of these species caught in standard test gang nets suggest that the population of cisco is approximately three times greater than that of lake whitefish. This difference in relative abundance may partially explain the higher incidence of cisco in the diet of northern pike. Both Lawler (1965) and Roberts (1975) report extremely low frequencies of occurrence of coregonids in the diet of northern pike in Heming and Cold Lakes respectively. Lake whitefish do occur at low levels in Kakisa Lake northern pike (approximately 2.2% occurrence in feeding fish), which agrees with the findings of Roberts (1975). Cisco occur more frequently than any other fish in the diet of Kakisa Lake northern pike. The average frequency of occurrence in feeding fish is approximately 18%. In the studies of Lawler (1965) and Roberts (1975) cisco were found to be of minor importance in the diet. Miller (1956) reports the average fork length of Cold Lake cisco as 20 to 25 cm, which is similar to the size of those from Kakisa Lake. Thus size does not seem to explain the different levels of occurrence of cisco in the diet of northern pike from Cold and Kakisa Lakes. Roberts (1975) notes that over the summer cisco become less common in the littoral region of Cold Lake; in Kakisa Lake cisco become more abundant in the shallows as the summer progresses. This difference in distribution appears to account for a large portion of the disparity between the frequency of occurrence of cisco in the diet of northern pike from these two lakes.

The phenomenon of differential importance of a prey species to northern pike from different lakes appears to exist for most other species of prey fish. This further points to the importance of relative abundance of prey in determining the diet of northern pike.

Data from Lamoureux (1973) and the present study indicate that walleye are approximately equal to lake whitefish in abundance in Kakisa Lake. Hoogland _et al_ (1956) indicate that northern pike encounter considerable difficulty in swallowing spiny prey fish. Given the relative population size and the deterrent offered by their spines, it would seem that walleye should have little importance in the diet of the northern pike from Kakisa Lake. This is not the case, since walleye were eaten more frequently than most soft-rayed species of fish present (Figure 12). Apparently these predators show some selective preference for walleye.

White suckers were the second most important food fish in both years of the study (Figure 12). The population of this species appears to be approximately one-half that of the lake whitefish or walleye. The frequency of occurrence of white suckers in the diet of northern pike is higher than would be expected on the basis of total numbers. Netting data suggest that this prey species is largely restricted to the littoral areas in Kakisa Lake, a trait which would make it more available to northern pike.

The low frequency of occurrence of burbot in the diet seems to be a result of the extremely low population levels of this species in Kakisa Lake. The relatively large size of individuals taken by northern pike accounts for the importance of this species in the diet.

Cannibalistic activities contribute significantly to the diet. The high density and wide range of sizes of northern pike in the littoral areas of the lake might suggest an even higher occurrence of this phenomenon. The explaination for the low frequency of cannibalism appears to relate to the behavior of small northern pike when confronted by potential conspecific predators. This topic will be discussed further in relation to behavioral observations.

Feeding on trout-perch and ninespine stickleback corresponds with the levels of relative abundance of these prey.

Specific information on population levels of these fish is lacking, therefore quantitative substantiation of this trend is not possible. However, seasonal changes in occurrence of these species in the diet of northern pike do lend qualitative support to the relative abundance hypothesis.

Spottail shiners are the most abundant forage fish in the littoral region of Kakisa Lake. The approximate average number of spottail shiners seen on the 22 meter long, Muskeg River transects was 235. Northern pike were often noted in the immediate vicinity of the transects, yet in northern pike stomachs examined, spottail shiners never attained a frequency of occurrence above 10% in any month. This paradoxical situation may arise as a result of the predation reducing attributes of spottail shiner schooling behavior, as suggested by Nursall (1973).

For most prey species the level of occurrence in the diet of northern pike appears to depend on the level of relative abundance of the particular species in the littoral zone. These findings are in agreement with those of Frost (1954) and Ivanova (1969). Walleye, spottail shiner, and northern pike represent exceptions to this trend. Selective feeding by northern pike appears to operate in the case of walleye. Reduced availability, resulting from unique behavioral traits, explains the lower than expected levels of occurrence of northern pike and spottail shiners in the diet.

3. Seasonal Changes in Diet

The spring to autumn rise in frequency of occurrence of cisco in the diet of northern pike (Figure 13) appears to be a result of increases in abundance of this prey in the shallows of the lake. Shallow water gill net catches of cisco show a corresponding increase over the same period. It seems that this fish gradually increases its inshore feeding over the summer, and as a result becomes more available to northern pike. The high incidence of cisco in northern pike stomachs during mid to late August is perhaps a result of incipient, prebreeding movements of this prey fish toward its inshore spawning grounds. This is suggested by the high proportion of gravid female cisco consumed at this time. This pattern of consumption of cisco is in contrast to that found in deeper lakes. Roberts (1975) finds that Cold Lake cisco move to deeper areas during the summer months, which would result in a decreased availability to northern pike, and hence less frequent occurrence in the diet.

Shallow water gillnet catches of white suckers in Kakisa Lake averaged 7.3 fish/net in June, 10.4 fish/net in July, and 3.1 fish/net in August. This pattern of relative abundance follows the rise and decline in occurrence of this species in the diet of northern pike (Figure 13). Lawler (1965) finds the occurrence of white suckers in northern pike stomachs remains below 10% throughout the summer period, but rises during the winter. He suggests that a seasonal spatial separation of northern pike and white suckers depresses the observed rate of predation. It appears that Kakisa Lake white suckers do not remain off shore during the whole summer period. This factor may account for the high frequency of occurrence of this prey in the mid to late summer diet of northern pike from Kakisa Lake (Figure 13).

Following the low level of occurrence during the spawning fast, the incidence of walleye in the stomachs of northern pike remains fairly constant over the summer (Figure 13). This testifies to the evenness of distribution of this prey fish throughout the lake, and its consistency of habits during the summer period. Lawler (1965) and Roberts (1975), both working on lakes deeper than Kakisa, found walleye to be infrequent in the summer diet of northern pike. Makowecki (1973), studying Seibert Lake (maximum depth 11 m), found walleye to have a summer average occurrence of 2.8% in northern pike. In Kakisa Lake, the shallowest of these four lakes, the average frequency of walleye in the diet of northern pike was 9.4%. Walleye remain in the deeper regions during the day in lakes which thermally stratify and have low turbidity in the summer (Scott and Crossman, 1973). In shallower lakes, such as Kakisa, which have low transparency and isothermal conditions during the summer, walleye range into shallow littoral areas, and extend their activity periods into the daylight hours. This presumably explains the continued high level of importance of walleye in the diet of northern pike throughout the summer in Kakisa Lake.

The temporarily high densities of northern pike around the mouths of the spawning streams in May would result in and increased opportunity for acts of cannibalism. With dispersal of fish, the incidence of cannibalism declines to a stable, lower level through June and July. A slight rise again in August correlates with increased feeding on young of the year. These fish have attained a sized acceptable for predation, and thus are occasionally consumed. The pattern of cannibalism observed appears consistent with the findings of Frost (1954) and Lawler (1965).

During May, trout-perch were the most frequently consumed prey fish (Figure 13). In the spring, this species moves shoreward, and forms spawning aggregations in the littoral region (Scott and Crossman, 1973). Frost (1954) explains that such "congregations of breeding fish are easy prey for northern pike." Up to nine ripe female trout-perch were found in a single northern pike stomach during this period. The development of a spawning fast in the northern pike population may have precluded an even greater utilization of this abundant and available forage fish during May.

From June to August the numbers of trout-perch increase in the diet. This species inhabits offshore areas during the daylight hours, and moves shoreward during the dusk to dawn period (Paetz and Nelson, 1970). With increasing duration of the night, following the summer solstice, trout-perch should remain inshore for correspondingly longer periods. This would increase their availability to northern pike, and account for the highest level of consumption reached in August (Figure 13).

Spottail shiners show a low but stable frequency of occurrence in northern pike stomachs throughout the summer (Figure 13). Lawler (1965) reports the existence of a similar situation in Heming Lake. In Kakisa Lake the species tends to be abundant in the littoral region throughout the summer, apparently in excess in relation to utilization by northern pike.

Ninespine stickleback are pelagic in lakes during the spring period (Scott and Crossman, 1973; pers. observ., Kakisa Lake). This is reflected in their complete absence from the diet of northern pike during May (Figure 13). During June, ninespine sticklebacks move into littoral regions to breed. At this time they achieve their maximum level of occurrence in the stomachs of northern pike. This situation is similar to that found in Cold Lake by Roberts (1975), who reports a preponderance of gravid female ninespine sticklebacks in the diet at this time. Decreased availability, as a result of termination of breeding and subsequent dispersal, seems to account for lower occurrence of ninespine stickleback in the diet of northern pike for the rest of the summer. Lawler (1965) finds this prey to occur infrequently in the diet over the entire summer, with no peaks associated with its breeding activities.

Amphipods and odonatans comprise the majority of invertebrates consumed during May (Figure 13), when invertebrates in general attain their highest occurrence in the diet. Late instars of these two major groups are abundant in the vegetated shallows of the lake and spawning rivers during May and June (D. Musbach, pers. comm.). Lamoureux (1973) indicates that large amphipods decline in abundance in Kakisa Lake over the summer. This parallels their decline in the diet of northern pike. Odonatans show a similar decline in the diet, presumably as a result of the depletion of the final nymphal instars which emerge as adults. Other invertebrates (Figure 13) are mainly Hirudinea, trichopterans, and ephemeropterans. This general group declines more gradually over the summer, since only a portion of the organisms included in this category emerge from the aquatic environment. A portion of the decline of invertebrates in the diet over the summer is likely owing to the increase of piscivorous tendencies in the predator population.

4. Predator Size and Diet Composition

The findings of Frost (1954), Beyerle and Williams (1968), and those of the present study all suggest that the diet of northern pike changes with growth of the predator. Spatial separation of certain size groups of northern pike from some prey species is partially responsible for the changes observed. Also important is the increase of preferred prey size with increase in predator size, as noted by Nikolsky (1963), Johnson (1969), and others.

Cisco which first appear in the diet of 30-39 cm northern pike are of age classes 1+ and 2+. Young of the year of this prey species were never obtained from the shallows of Kakisa Lake by trawling or seining. This apparent avoidance of the littoral zone by young cisco may explain their absence from the diet of 20-29 cm predators (Table 3). Cisco were prominent in the diet of all larger size classes of northern pike, reaching a peak in the 50-59 cm size class. Cisco in Kakisa Lake seldom exceed 150 gm or 25 cm in fork length, with average length being 18 cm. Optimum prey size values given by Hoogland _et al_ (1956) and Nursall (1973) predict the high importance of these stunted cisco in the diet of the 40-49 and 50-59 cm size classes of northern pike. Cisco never attain a size sufficiently large to make them invulnerable to predation by northern pike in Kakisa Lake. This fact, coupled with the very large cisco population, may account for the commonness of this species in the diet of northern pike.

White suckers follow a pattern of occurrence similar to that of cisco (Table 3). The lack of importance of white suckers in the diet of 20-29 cm northern pike may be a result of a spatial separation from the predator, as suggested by Lawler (1965). In Kakisa Lake, young white suckers frequent gravelly or sandy shore lines and the outer edges of macrophyte beds. Most small northern pike frequent very shallow areas of emergent aquatic vegetation. Hence contact between the young of the two species may be minimal. Also, it appears that schooling behavior of young white suckers may reduce their availability to young northern pike. Increase in size of this prey is accompanied by a diminution of integrated schooling tendencies, and presumably a reduction in the protection from predation afforded by this habit. As a result the intermediate sizes of white suckers are most available to northern pike, and are consumed more frequently than the other size classes of the species (Table 3). However, the rapid growth of white suckers acts to reduce predation on older fish by increasing their size to the point where they are too large to be ingested by all but the largest predators.

Small lake whitefish were rare in the littoral regions of Kakisa Lake, while larger individuals (age 3+ years and older) did move into the littoral regions. This situation is similar to that described for white suckers, and presumably, similar factors control the pattern of consumption of lake white fish by northern pike (Table 3).

Netting and seining operations indicate that most age classes of walleye above 0+ are distributed throughout the entire lake. Their occurrence in the stomachs of all size classes of northern pike is likely a result of this general distribution. Walleye are found most often in the largest northern pike (Table 3). This substantiates findings of Frost (1954), which indicate that the percentage of spiny prey consumed increases with increasing size of northern pike.

Burbot are absent from the diet of northern pike of less than 40 cm fork length (Table 3). During the early years of life burbot inhabit open shore lines, where they remain hidden beneath rocks and debris (Scott and Crossman, 1973). Open areas are rarely frequented by northern pike in Kakisa Lake, hence they would rarely encounter small burbot. Older burbot are benthic in the pelagic regions of most lakes (Lawler, 1963). A small number of mature individuals were observed in the littoral regions of Kakisa Lake, where they would have been available to northern pike. The large size of the burbot seen would seem to restrict their availability to only the largest northern pike. This is borne out by data (Table 3) indicating that burbot are most heavily preyed upon by 60-69 cm northern pike.

Cannibalism occurs at low levels in most size classes of northern pike in Kakisa Lake (Table 3). This is similar to the situation in Lake Windermere (Frost, 1954). The reason for the absence of cannibalism in the 30-39 cm size group is not immediately apparent. Possibly a change in general habitat preference separates this group from smaller conspecifics which could act as prey.

The patterns of consumption of trout-perch, spottail shiner, and ninespine stickleback all illustrate clearly the shift in diet of growing northern pike (Table 3). The maximum sizes attained by these three prey species are not sufficiently large to prevent predation by even the 20-29 cm predators. These prey species all show a similar pattern of highest frequency of occurrence in the diet of 20-29 cm northern pike. Their occurrence then declines gradually through each successively larger size class of predator. This pattern is also evident in the consumption of invertebrates. Frost (1954) found and inverse relationship between percent occurrence of both the minnow Phoxinus phoxinus and invertebrates, and the size of northern pike. In Heming Lake, spottail shiners decline in their frequency of occurrence in the diet with increase in size of northern pike (Lawler, 1965). Lawler (1965) and Roberts (1975) do point out exceptions to this general trend. They both report trout-perch to be of high importance to northern pike from 20-69 cm fork length. In these cases the larger predators are utilizing small prey which are aggregated and available. The small size of prey is compensated by an increase in the numbers consumed by successively larger northern pike. In Kakisa Lake a similar situation develops temporarily in June when spawning ninespine sticklebacks are consumed by most sizes of northern pike.

5. Predator-prey Size Relationships

The effects of predator size on diet composition have been discussed in the preceding section, hence specific prey species will not be considered here.

Prey size relative to size of northern pike has been discussed by Frost (1954), Nikolsky (1963), and Popova (1967). Absolute prey length is found to increase concomitantly with predator length, as reported by all three workers. Popova (1967) also states that relative prey length declines with increase in length of predator. This is in disagreement with the findings of the present study (Table 4). Relative prey size is slightly lower for intermediate sized northern pike, but rises to its highest level in the largest predators. The existence of a relationship between relative prey size and predator size must depend upon the size classes of prey available. Absence of certain size classes of prey could change the pattern of this relationship, a fact which may explain the conflicting findings of Popova (1967). The overall average prey length to predator length ratio of 0.27 for Kakisa Lake northern pike agrees closely with the figure of 0.25 reported as optimum by Nursall (1973).

The relationship between maximum body depth of prey and mouth width of northern pike is much more constant than that of prey length and predator length. During the present study, and those of Johnson (1969) and Roberts (1975), northern pike were occasionally found with prey fish, too long to swallow completely, protruding beyond their jaws. Also, it is apparent that forage fish species consumed are of a variety of body forms, with some species having a greater depth to length ratio than others. These two factors tend to obscure the pattern of size related predation if length of prey is the criterion used. The body depth to jaw width ratio indicates clearly that size selective predation is an intrinsic trait of northern pike, where the opportunity is available. The overall average ratio of prey depth to jaw width of northern pike from Kakisa Lake was 0.49, which agrees well with the value of 0.50 to 0.59 obtained by Johnson (1969). These data indicate that the relative size (body depth) of prey consumed increases with predator size (Table 5). This finding is in disagreement with the suggestion of Ivlev (1961), who without qualifying stated, "that predators of all size classes prefer to devour victims of the largest size possible."

The problem of the significance of prey size relative to predator size is complex because of the numerous variables involved, and studies on the subject are lacking. Davis and Warren (1968) state that they "know of no reliable information on the changes in the relationship between food consumption and growth with change in age or size of the fish." Johnson (1966a) does state that the relative maintainance requirements of northern pike increase with size, in natural populations. There is also some suggestion that the predatory act itself may become metabolically more costly for larger fish. Brett (1965) states:

> "There is a rapid decline in the relative ability to maintain a sustained swimming speed as fish size increases. This decay occurs despite a relative increase in body musculature (45% for 30 g; 60% for 1500 g) and a progressive increase in metabolic scope. Even with these assets it is apparent that the hydrodynamic drag which accompanies increased size is only partially met. The metabolic process is not a match for the great energy cost of sustained high speed for large fish.

On the basis of this information it appears that it may be necessary for larger predators to select prey which approach more closely the maximum size ingestible, in order to reduce the number of predatory acts required to become sated. In smaller predators the predatory act itself is relatively less costly, due to the significantly lower relative energy loss from pursuit. Thus a small predator could feed economically, using a number of predatory acts, on relatively smaller prey, which would be more frequently encountered owing to their great numbers.

The differences in the relative sizes of prey consumed by male and female northern pike of the same length (Figure 14) is significant in two respects. Firstly, it is likely that this habit functions as an immediate means of reducing competition between the sexes. This is accomplished by allowing the species to broaden the resource base upon which it depends. The differences between the diets of males and females (Table 6) suggest that this is occurring in the Kakisa Lake population. Schoener (1967) has found differences between the diets of male and female lizards of the genus Anolis. These he attributes to a relatively larger head size in males. The differences in feeding by male and female northern pike may also function as an ultimate means of reducing competition by enhancing the development of the sexual dimorphism in body size. Secondly, because of the higher metabolic expenditure of females (suggested by Casselman, 1975) related to gonadal development, it may be necessary for this sex to consume relatively larger prey. This would allow for a higher efficiency of predation, by reducing capture costs, and thus free more nutrient for gonadal production and growth.

III Behavior

A. General Activity

RESULTS

The basic behavior pattern of northern pike was typified by extended periods of inactivity punctuated by periods of activity of variable length. Northern pike were active for approximately 20 to 40% of the daylight hours; the remaining daylight hours were spent inactive, with no locomotory behavior occurring. The values given are averages, since day to day fluctuations in activity were typical of all fish studied. For the purposes of this study a fish was considered to be active if it exhibited movement as a result of locomotory behavior for a period of greater than 10 seconds. Conversely, a fish was considered to be inactive if it exhibited no movement due to locomotory behavior for a period of at least five minutes. This system was employed since northern pike occasionally made very minor postural adjustments during extended periods of inactivity, and executed frequent, brief stops during extended periods of activity. Very slight movements of the paired and median fins, used to maintain balance while stationary, were not considered to be locomotory movements.

1. Locomotory Behavior

The locomotory movements of northern pike can be separated into four basic types, forward locomotion, backward locomotion, turning, and stopping. The specialized movements and postures associated with predatory and social activities will be considered separately. Swimming speeds listed, were determined by timing the travel of fish over a known distance in the observation area.

Forward movement

Forward movement by northern pike was produced in two basic manners, depending upon the speed of travel undertaken.

Slow forward movement, approximately 0.05 m/sec or less, was produced by means of sculling movements of the pectoral fins. The posterior borders of the dorsal and anal fins swept delicately from side to side, producing additional forward thrust. Forward movement produced in this manner allowed the trunk of the fish to remain straight. The term "sculling locomotion" will be used to denote this type of swimming.

The second mode of forward locomotion, basic to all faster swimming, involved the passage of a wave along the trunk of the fish, increasing in amplitude towards the tail. These body undulations moved the caudal, dorsal, and anal fins back and forth across the midline of the long axis of the body. In this type of locomotion the pectoral and pelvic fins were held close to the body. Several categories of swimming employing this type of locomotion could be distinguished. Slow cruising, approximately 0.05 to 0.25 m/sec, was the slowest and most frequently observed form. Moderate or intermediate swimming, 0.25 to 0.75 m/sec, was used by northern pike approaching objects in the water (ie. other fish, prey organisms). Burst swimming, 1.0 to 2.5 m/sec, was used mainly in predatory and fright reactions. Gray (1957) lists the maximum observed swimming speeds of northern pike as 1.5 to 2.1 m/sec.

Backward movement

Backing up was observed to occur when northern pike were moving out of confined spaces where forward movement was not possible, and also occasionally during social and predatory activities. The propulsive force for this type of movement was produced with all fins except the caudal fin. The body was held straight, as in slow forward sculling. The pectoral fins reversed the forward sculling motion, thus directing the propulsive force forward. The pelvic fins were employed in a similar manner, but their movements appeared weaker than those of the pectorals. The posterior borders of the dorsal and anal fins were flexed laterally and anteriorly repeatedly to one side. Backward movement was slow, probably less than 0.05 m/sec.

Turning

Northern pike employed two methods of turning. The first method was used when a stationary or very slow moving fish executed a slow turn. In this case the body of the fish remained straight, while the pectoral, pelvic, and median fins produced the propulsive forces. The paired fins swept forward on one side of the body while sweeping backward on the other side. The propulsive forces, thus produced, imparted lateral torque to the body. The posterior borders of the median fins were repeatedly reflexed laterally in unison to the side of the body having the paired fins pointing forward. The second method of turning was employed when fish were swimming using caudal peduncle propulsion. The turn was produced by projecting the paired fins on one side of the body laterally in the vertical plane, while the caudal peduncle was flexed sharply to the same side. This caused an abrupt turn, the sharpness of which was determined by the degree of flexion of the caudal peduncle.

Stopping

The cessation of forward movement could occur passively by termination of locomotory movements, and consequent gliding to a stop. Movement was also stopped by projecting the paired fins laterally in the vertical plane. This was accompanied by flexion of the caudal peduncle laterally. The strength and magnitude of these movements determined the abruptness of the stop.

2. Activity and Habitat Utilization

Three general habitat types were available within the observation area. 1. Vegetated habitat was defined as areas having dense submergent or emergent beds of aquatic macrophytes, with plant coverage of approximately 30% or greater. 2. Cover habitats were those areas with less than 30% plant cover directly under overhanging riparian vegetation, and all areas within 0.3 m of the outer borders of aquatic macrophyte beds. 3. Open habitat was the area with no plant cover.

Slow cruising behavior comprised 62.5% of daytime locomotory behavior (Table 7). While cruising, northern pike stayed close to or in the edges of macrophyte beds, and close to shore near overhanging riparian vegetation (Vegetation and Cover; Table 7). Excursions into open water had a frequency of 19.6% (Table 7), slightly less than one half that shown for cruising in cover. These findings are substantiated by observations made while Scuba diving in the littoral regions of the open lake. Here, northern pike tended to confine their activities to regions of aquatic vegetation by swimming parallel to the outer borders of these areas.

Moderately fast swimming and burst swimming had

Table 7. Summary of activities and habitats used by eight northern pike while active. Observations were made at five minute intervals during activity periods. The data are taken from 695 hours of fish observation. Values indicate number of separate times specified activity was observed in a specific habitat type.

	Sculling	Cruising	Moderate Swimming	Burst Swimming	Turning	Totals
Open	102	366	26	9	104	607
	(5.5%)	(19.6%)	(1.4%)	(0.5%)	(5.6%)	(32.6%)
Cover	152	729	15	5	174	1075
	(8.1%)	(39.1%)	(0.8%)	(0.3%)	(9.3%)	(57.6%)
Vegetation	27	121	5	5	24	182
	(1.4%)	(6.5%)	(0.3%)	(0.3%)	(1.3%)	(9.8%)
Totals	281	1216	46	19	302	1864
	(15.0%)	(65.2%)	(2.5%)	(1.1%)	(16.2%)	

frequencies of occurrence of 2.5% and 1.1% respectively (Table 7). Unlike cruising behavior, these activities occurred most frequently in open water. These behaviors were associated with observable external stimuli, in most cases. Generally, these types of locomotion were employed during predatory, social, and escape behaviors. Natural escape responses by northern pike were observed on five separate occasions. Two resulted from the activities of a muskrat (Ondatra zibethicus) in the observation area, and three were a result of the activities of a belted kingfisher (Megaceryle alcyon) over the stream. In all cases the northern pike involved employed burst speed swimming to move away from the area of disturbance to the cover of aquatic vegetation.

Sculling and turning movements occurred as normal components of general locomotory activity. Both tended to occur least frequently in vegetated areas (Table 7).

On the basis of relative areas of each habitat type available in the observation area, a theoretical expected utilization value for habitats was obtained. Comparison of actual utilization of each habitat, during activity, to the theoretical expected utilization yields a utilization index (UI) for each habitat type (Table 8). Values of the UI are greater than zero, with values less than one indicating avoidance, and values greater than one indicating a selective

Table 8. Observed and expected use of habitat by eight northern pike while active. Habitat utilization index values greater than 1.0 indicate preferred use, and values less than 1.0 indicate avoidance. Table values obtained by recording fish position once every five minutes during activity, total observation time 695 hours.

Habitat Types	Observed Utilization	Expected Utilization	Habitat Utilization Index
Open	607 (32.6%)	893 (47.9%)	0.68
Cover	1075 (57.6%)	399 (21.4%)	2.69
Vegetation	182 (9.8%)	572 (30.7%)	0.32

Table 9. Habitat location and behavior of northern pike prior to predatory acts. Values indicate number of individual times fish engaged in specified activity in a particular habitat prior to a predatory act. Chi-square test for independence applied. Abbreviation used: Veg = Vegetation.

	Habitat Location			
Behavior	Cover	Veg	Open	Totals
Active	20 (21%)	2 (2%)	7 (8%)	29 (31%) ⩓
Inactive	48 (51%)	11 (12%)	6 (6%)	65 (69%)
Totals	68 (72%)	13 (14%)	13 (14%)	94

⩓- Indicates significant difference at 1% level.

preference. From Table 8 it is evident that activity in vegetated areas was avoided (UI = 0.32). This would be expected since dense vegetation appeared to act as an impediment to locomotion. The UI value of 2.69 for areas of cover indicates a preferential use of this habitat type during activity periods. Areas of open water were avoided, or used less than expected, (UI = 0.68) by northern pike during activity.

3. Activity Patterns

Diurnal cycle

Northern pike held in the observation area exhibited a daily bimodal pattern of activity (Figure 15). The general pattern was similar over both summers (r = +0.85) from late May through August. Activity rose slowly through the morning hours and reached a peak around midday. This was followed by a decline in activity levels through the afternoon. A second slow rise occurred from midafternoon to a peak between 1600 and 1700 hours. This second peak was generally higher than the midday peak. Following the evening peak, the activity levels declined slowly, with occasional fluctuation evident.

Seasonal cycles

A seasonal shift in activity levels was also apparent (Figure 16). General activity was highest during the late

Figure 15. Diurnal activity patterns of northern pike. Values as percent of hour spent active, and averaged for all fish observed. Correlation between hourly activity levels in 1973 and 1974 is +0.85.

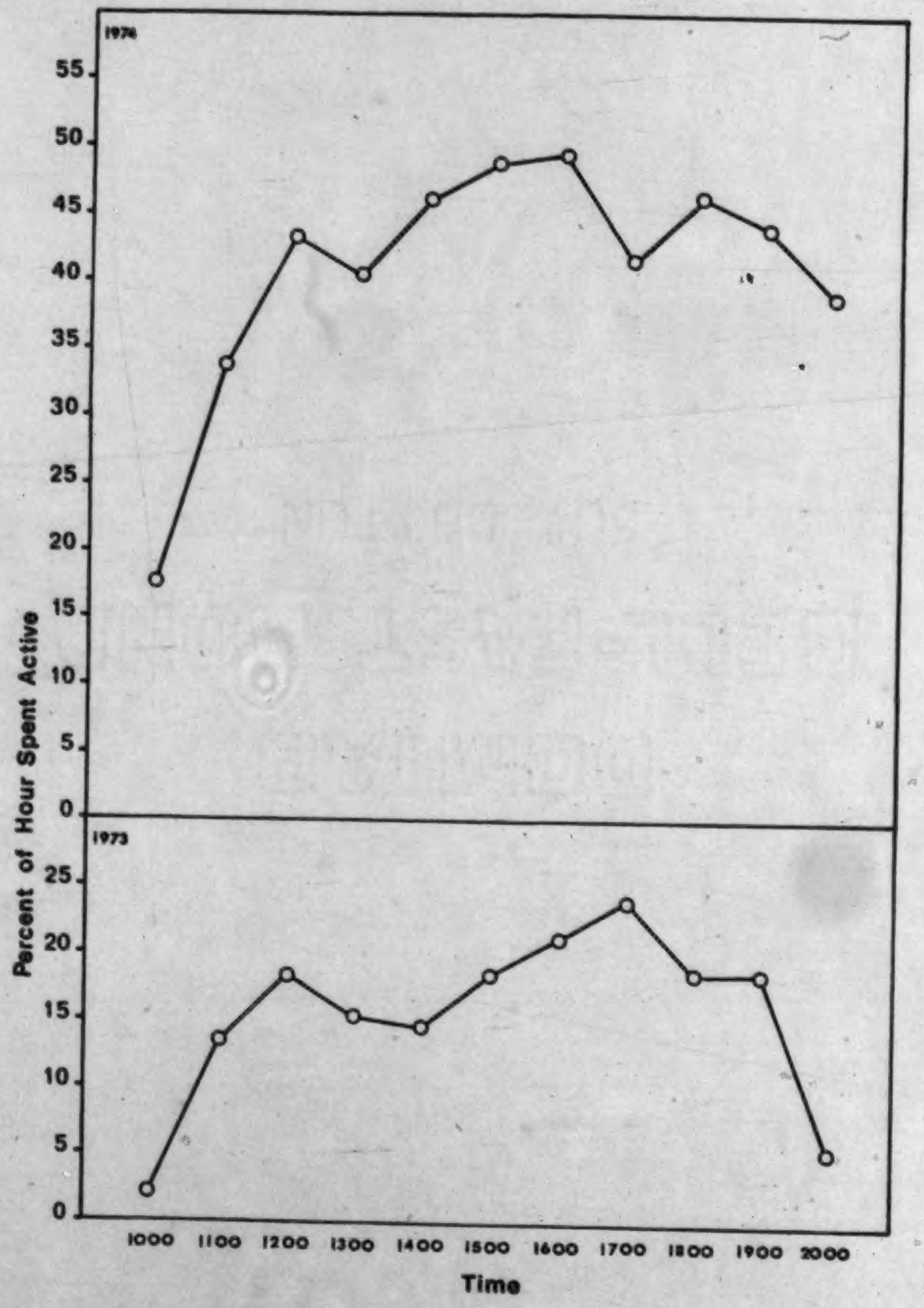
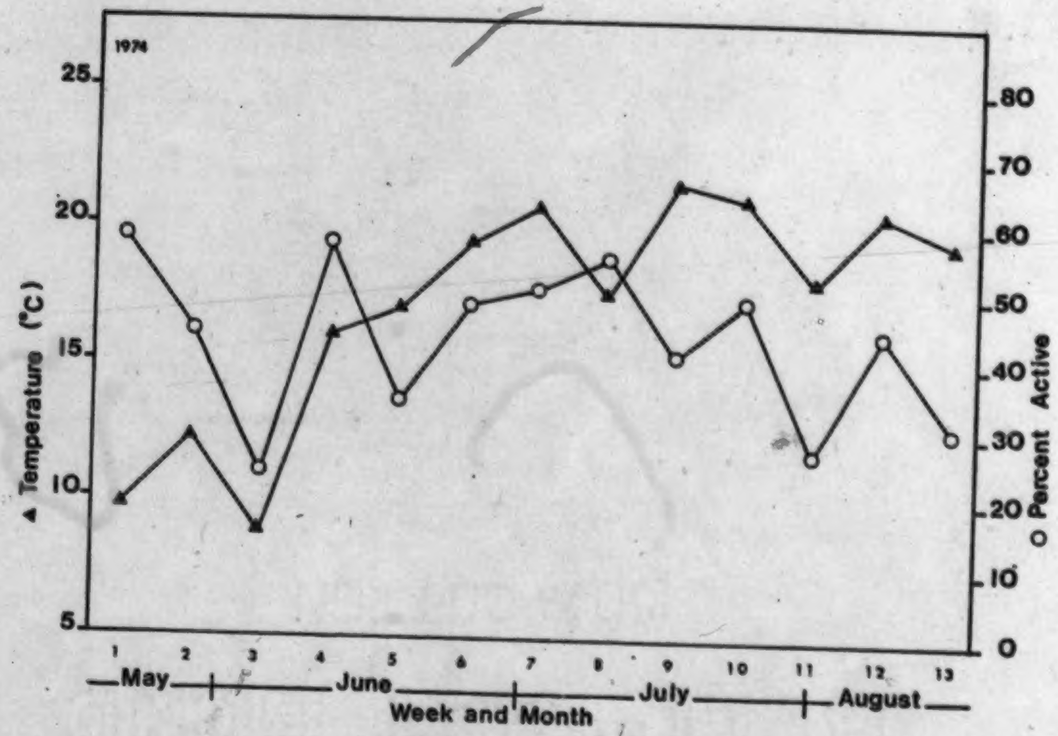
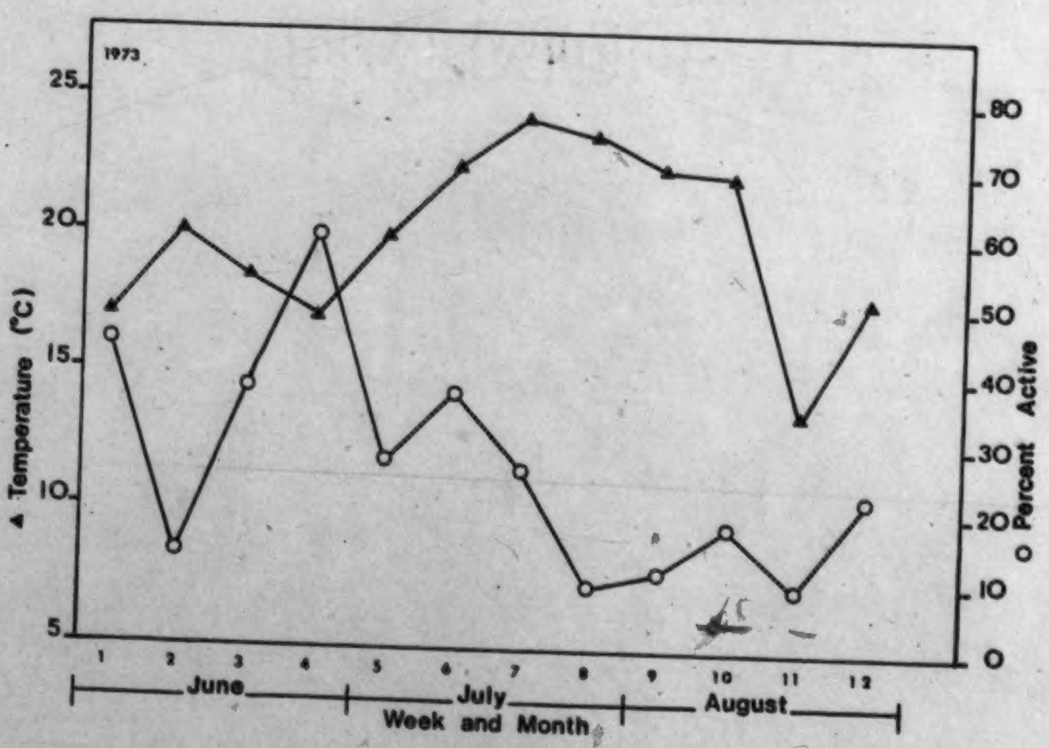

1974
1973
Percent of Hour Spent Active
55
50
45
40
35
30
25
20
15
10
5
0
25
20
15
10
5
0
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
Time

Figure 16. Average percent of observation period spent active during each week of the study, and mean Study Stream temperature for week. Correlation mean temperature and average activity : 1974 - r = +0.09 , 1973 - r = -0.26.


1974
25
20
15
10
5
▲ Temperature (°C)
80
70
60
50
40
30
20
10
0
○ Percent Active
1
2
3
4
5
6
7
8
9
10
11
12
13
May
June
July
August
Week and Month


1973
25
20
15
10
5
▲ Temperature (°C)
80
70
60
50
40
30
20
10
0
○ Percent Active
1
2
3
4
5
6
7
8
9
10
11
12
June
July
August
Week and Month

spring and early summer, but showed initial wide fluctuations in June. Activity levels fluctuated less widely and exhibited a general decline through July and August. Average weekly water temperatures plotted against activity (Figure 16) show no significant correlation that would explain the observed trend. The declining activity did tend to follow the decreasing day length after mid-June.

4. Inactivity and Habitat Preference

Northern pike were found to spend a major portion of the daylight hours inactive. This aspect of their behavior has a definite importance in relation to the predatory habits of the species, and by inference, to the energy economics of the species.

Inactive northern pike in open water above the substratum assumed a straight bodied posture, with the tail region held several centimeters lower than the head region. Paired fins were extended ventro-laterally and slightly anteriorly, and carried on weak sculling movements. In addition, the posterior borders of the dorsal and anal fins were delicately swept from side to side. When fish were inactive on the bottom, the pelvic, anal, and caudal fins appeared to act as the main points of contact with the substratum. The anterior portion of the body thus remained slightly elevated. Inactive northern pike in dense aquatic vegetation carried on little sculling, the support of the surrounding plants possibly aiding in the maintenance of upright posture.

While immobile, northern pike appeared to remain receptive to predatory stimuli. In 69% of the observed predatory acts the northern pike involved had initially been inactive (Table 9). The type of habitat utilized during inactivity periods relates to the predatory function of this behavior. In 63% of the total predatory acts observed northern pike had initially been inactive in cover areas or aquatic vegetation (Table 9).

An examination was conducted to determine the habitat preferences, if any, shown by northern pike during periods of inactivity. The three habitats available could be further subdivided by identifying three strata within each habitat type. These three strata were loosely defined as surface, middepth, and bottom. The amount and type of habitat available in the observation area was the same for both summers of the study.

Data indicate the existence of a highly significant difference ($p<0.001$) between the amounts of time northern pike spent in each habitat zone while inactive (Table 10). However, these data indicate only the total amounts of time spent in each of the habitat strata. To obtain an estimate of the habitat preference it was first necessary to determine the total availability of each stratum within the observation area, and to use this to calculate a theoretical utilization. Secondly, the theoretical values were compared to the actual observed levels of utilization of each habitat stratum. The result of this analysis is a habitat preference index (PI), which indicates the preference shown for each habitat category (Table 11). The PI indicates the selection of habitats as sites for inactivity, while the UI value (Table 8) indicates the use of various habitats while active. Recalculating the 'F' value indicates that there is a significant difference between the preferences shown for the different habitat strata ($p<0.001$). Northern pike displayed a distinct preference for surface cover areas while inactive, and the PI value of 3.84 is significantly higher than that shown for any other area (Table 11). Northern pike showed selective preferences for three other categories of habitat; these were bottom vegetation (PI = 2.34), surface vegetation (PI = 1.59), and bottom cover (PI = 1.43). Midwater cover areas and bottom open areas were used slightly less than expected, with PI values of 0.92 and 0.91 respectively. Areas of midwater in vegetation were partially avoided (PI = 0.55). Midwater and surface areas in open water were clearly avoided by northern pike during periods of inactivity, with PI values for these areas being 0.20 and 0.14 respectively.

Table 10. Habitat use by 12 northern pike while inactive. Values in minutes of use during 48.5 hours of inactivity for each fish. Abbreviations used: V = Vegetation, C = Cover, O = Open, S = Surface, M = Midwater, B = Bottom.

Fish	Habitat Category								
	VS	VM	VB	CS	CM	CB	OS	OM	OB
MP1	731	47	365	385	94	351	291	293	348
RT	464	309	219	817	342	477	32	204	41
LF	513	360	494	599	339	365	30	96	109
JP1	327	377	921	526	309	284	1	98	62
JJP1	375	190	506	322	407	531	71	96	407
B	330	336	205	1273	158	273	9	6	315
C	316	53	21	920	358	332	53	72	780
D	589	40	36	917	56	32	58	0	1177
E	310	24	0	751	174	299	285	106	956
F	1088	133	42	930	40	86	9	17	560
G	380	69	98	1286	172	390	47	48	415
W	154	15	334	1645	44	469	0	239	5
Mean	465	163	270	864	208	324	74	106	431

Analysis of Variance

	M.S.	F*	5%	1%
Between Habitats -	713386.3	12.54	2.05	2.72
Between Fish -	56881.6			

* There is a highly significant difference in the use of the various habitats by northern pike (total time).

Duncan's Multiple Range Test - Means underlined by same line are not significantly different at the 5% level

OS	OM	VM	CM	VB	CB	OB	VS	CS
74	106	163	208	270	324	431	465	864

Table 11. Summary of the habitat preferences shown by 12 northern pike during periods of inactivity. Values from Table 10 were used to calculate habitat preference indices listed in this table.

Fish	Habitat Category								
	VS	VM	VB	CS	CM	CB	OS	OM	OB
MP1	2.49	0.16	3.29	1.70	0.41	1.55	0.55	0.56	0.74
RT	1.58	1.05	1.97	3.60	1.51	2.10	0.06	0.39	0.09
LF	1.74	1.22	4.45	2.64	1.49	1.61	0.06	0.18	0.23
JP1	1.11	1.28	8.30	2.32	1.36	1.25	0.00	0.19	0.13
JJP1	1.28	0.65	4.56	1.49	1.79	2.34	0.13	0.18	0.86
B	1.22	1.14	1.85	5.61	0.70	1.20	0.02	0.01	0.67
C	1.07	0.18	0.19	4.05	1.58	1.46	0.10	0.14	1.65
D	2.00	0.14	0.32	4.04	0.25	0.14	0.11	0.00	2.49
E	1.05	0.08	0.00	3.31	0.77	1.32	0.54	0.20	2.02
F	3.70	0.45	0.38	4.10	0.18	0.38	0.02	0.03	1.18
G	1.29	0.23	0.88	5.67	0.76	1.72	0.09	0.09	0.88
W	0.52	0.05	3.01	7.25	0.19	2.07	0.00	0.45	0.01
Mean	1.59	0.55	2.43	3.82	0.92	1.43	0.14	0.20	0.91

Analysis of Variance

	M.S.	F*	5%	1%
Between Habitats -	16.66	13.12	2.05	2.72
Between Fish -	1.27			

* There is a significant difference in the preferences shown by northern pike for the various habitats.

Duncan's Multiple Range Test - Means underlined by the same line are not significantly different at the 5% level.

OS	OM	VM	OB	CM	CB	VS	VB	CS
0.14	0.20	0.55	0.91	0.92	1.43	1.59	2.43	3.82

DISCUSSION

In the observation channel, northern pike spent a major portion of the daylight hours inactive. Radio telemetry tracking studies have illustrated that similar tendencies are displayed by free ranging northern pike (Malinin, 1971). Wich (1958) and Fabricius and Gustafson (1958) also report observations of northern pike spending extended periods of time in a state of inactivity.

1. Locomotory Behavior

The locomotory activities of northern pike are essentially similar to those shown by most other teleosts of similar body form. Hoogland et al. (1956) have described the basic patterns of fins movements involved in locomotion of northern pike, and in all cases their descriptions are confirmed by present findings.

Sculling locomotion is produced by the activities of the fins only, with no body flexion involved. This form of locomotion is important in allowing the predator to move and orient itself slowly and precisely with stealth. Such ability seems essential to certain orientation and stalking components of the predatory act.

Locomotion employing body flexion is evident in all faster types of forward swimming. Slow cruising is the form most frequently employed (Table 7). It is exercised by fish during general activity periods, and its inception appears to require no external eliciting stimuli. However, it seems that light may function as a Zeitgeber in this case, since a loose diurnal cycle of activity is evident (Figure 15). In many situations the behavior functions primarily in movement to a new location, where the fish again reverts to an inactive state. During slow cruising, northern pike, at times, are receptive to predatory and social stimuli. Thus it might be proposed that in these cases the activity represents appetitive behavior directed towards the procurment of food or social interactions. Schoener (1969) notes that in pure pursuers, such as northern pike, the search for food costs nothing above what would be normally expended on other activities anyway. Hence it seems that cruising behavior could fulfill a number of functions, with the specific type dependent upon the stimuli encountered. As a result, from present data it is not possible to suggest what specific, incipient drives are responsible for initiation of this behavior in different cases.

Moderate speed locomotion is the second most frequently observed form of swimming employing body flexion. This faster type of locomotion has a significantly lower frequency of occurrence than slow cruising (Table 7). Moderate speed locomotion is elicited, in most cases, by apparent external stimuli. It is frequently employed during the approach to objects or points of stimuli, such as prey, other northern pike, or disturbances in the water. Occasionally, moderate speed locomotion is undertaken when apparent external stimuli are lacking. In most of these situations the behavior occurs during the performance of display-like activities, which may represent displacement behaviors (Tinbergen, 1952).

Burst speed swimming invariably arises as a result of external stimuli. This form of locomotion has the lowest frequency of occurrence of the three body flexion types (Table 7). It mainly occurs in predatory and fright reaction, but also occasionally is manifest during social interactions. The deeply forked caudal fin and caudally placed dorsal fin of northern pike suggest that the fish is adapted for rapid swimming. Gosline (1971) suggests the functional importance of these anatomical features. He states:

> "In fast moving fishes, the greater wake presumably creates a more serious problem (of turbulence around the tail), and Alvee (1963) suggests that the broadly forked tails of such fish permit at least the outer parts of the caudal lobes to project into undisturbed water above and below the wake area."

During burst speed swimming the amplitude of tail beats decreases while their frequency increases, and this is accompanied by a similar decrease in the side to side movements of the head. This basic action-reaction phenomenon could have importance, especially during pursuit of prey, since it would allow the predator to maintain an accurate aim on the fleeing fish.

2. Activity and Habitat Utilization

During activity periods northern pike tend to remain in areas of cover (Table 8). This is accomplished by directing a major portion of the cruising activity along bank areas with overhanging riparian vegetation, or along the outer borders of aquatic macrophyte beds. These findings are in agreement with those of Malinin (1971) and Machniak (1975), who both suggest that northern pike tend to remain close to areas of aquatic vegetation during the daylight hours. This habit appears to have a number of benefits. First, cover seems to be important for the success of predatory acts of northern pike. Second, remaining in cover should afford a degree of protection from aerial predators. Third, abundant cover decreases the frequency of visual contact between individuals, which may be important in maintaining low levels of aggressive interactions even at high population densities.

Areas of open water are avoided by northern pike during activity periods (Table 8). This is primarily a result of a reduction of cruising activity in this habitat to less than one-half the level in cover habitat (Table 7). Sculling and turning activities also occur less frequently in open water, since the absence of physical barriers necessitates fewer course changes. The levels of moderate and burst speed swimming are highest in areas of open water (Table 7). This results from the high number of predatory and social acts which are initiated from areas of cover or vegetation, and are directed toward open water.

Northern pike do travel through areas of aquatic vegetation, but prolonged periods of activity do not occur in this type of habitat. Hence, locomotory activities are least frequently observed in these areas (Table 8). The impediment to locomotion offered by dense stands of aquatic macrophytes is likely responsible for an avoidance of activity in these areas.

3. Activity Patterns

A daily bimodal pattern of activity was characteristic of both study fish populations examined. The midday and evening peaks in activity (Figure 15) are similar to those reported for northern pike by Carlander and Cleary (1949) and Poddubnyi _et al_ (1970). Poddubnyi _et al_ (1970) agree that the evening activity peak is usually higher than that occurring at midday. This appears to correspond to the findings of Ivanova (1969), which indicate that when feeding conditions are not exceptionally good northern pike tend to shift their feeding activities toward the evening period. Malinin (1970) also reports activity peaks occurring at midday and evening. His data also indicate the existence of an early morning peak prior to sunrise. Since present observations were by needs restricted to the daylight hours, the occurrence of such a predawn peak in activity would not have been detected. However, two 24 hour netting studies conducted in 1974 did not indicate the occurrence of a predawn peak in activity in the lake population of northern pike.

Mean activity levels of northern pike tend to follow a seasonal pattern also. Generally, activity is highest in the spring following spawning, but fluctuates widely. In early summer levels become more stable, and then undergo a gradual decline through July and August (Figure 16). The high activity levels in May and June could be the result of an urge to return to the lake area following spawning. Miller (1948) and Makowecki (1973) both provide evidence indicating that northern pike may undertake substantial migrations at this time. An increased feeding drive following the spawning fast has been documented by Frost (1954) and Lawler (1965), and this too could contribute to the higher levels of activity observed in the spring. The gradual decline in activity through the summer is not well correlated with water temperatures. Johnson (1966a) finds a similar pattern of decline in maintenance requirements of northern pike over the same period, and this too is not well correlated with water temperature. It appears that the decline in activity through the latter portion of the summer corresponds to the decreasing day length following the summer solstice. This same conclusion is reached by Johnson (1966a) to explain the decline in maintenance requirements over this period. A further indication of basic physiological changes that may be occurring at this time is found in the work of Swift (1955). He determined that thyroid activity in brown trout (*Salmo trutta* L.) is at a maximum in mid to late June, and declines thereafter. He notes that this corresponds to the period of peak physical activity for the species. Swift (1955) postulates that the thyroid hormone exerts a tonic effect on the whole nervous system, rendering the animal more responsive to external environmental stimuli.

4. Inactivity and Habitat Preference

It is likely that extended periods of inactivity are an integral component of the predatory strategy of northern pike, which is basically one of "ambush predation" (Fortunova, 1959). Data pertaining to predatory activities indicate that a major portion of the predatory acts are undertaken by fish which were previously inactive (Table 9). Schoener's (1969) theory of optimal predatory strategies suggests that a predator, to achieve efficiency, must decrease energy expended in search or pursuit of prey. It seems that the low activity levels of northern pike can allow this predator to comply with both of these criteria, at least partially. Firstly, energy expended in searching for prey is obviously minimized by adopting a strategy which allows the prey to come to the predator. Secondly, energy expended in pursuit is perhaps reduced by allowing the prey to approach with in a short distance, thus permitting a short range strike by the predator. The energy conserved in these manners should allow northern pike to attain a fairly high predatory efficiency. This thesis is confirmed by the work of Johnson (1966a), which indicates that the maintenance requirements of this species are exceptionally low, while the rate of conversion of food to body weight is high. Nursall (1973) states:

> "The solitary pike probably requires abundant prey to thrive, for without it the ranging of pike to seek food must increase greatly with extra energy expenditure. Under such circumstances one might expect selection for increased hunting efficiency and for capture of larger prey."

Findings of the present study largely agree with these suggestions. In addition, data will be discussed later which indicate that, within limits, northern pike may react to prey shortages by restricting rather than increasing activity. It seems that the avoidance of excessive hunting activity may be one of the chief ways in which predatory efficiency is increased.

The importance of concealment as a requirement in the predatory act of northern pike is also apparent from data collected (Table 9). The majority of predatory acts observed (86%) were initiated, by moving or stationary fish, from areas of cover or vegetation. This would appear to comply with the requirement of allowing the prey to approach within a short distance of the predator. Nursall (1973) notes that prey are generally aware of northern pike in the open, and that this causes forage fish to modify their behavior accordingly. Present observations indicate that most prey fish show no modification of behavior when near a northern pike which is concealed in vegetation or cover, which can be taken to imply that prey have not detected the predator. These findings strongly disagree with the suggestion of Mauck and Coble (1971), that availability of cover does not effect the vulnerability of prey to northern pike predation.

In keeping with the thesis which suggests that certain benefits accrue to northern pike from the use of specific habitats, it was assumed that habitat preferences should be shown during periods of inactivity. Individual fish do exhibit propensities to spend inactivity periods within certain types of habitat (Table 10). As predicted, northern pike do spend disproportionate amounts of time, during inactivity periods, in certain habitat stratum (Table 11).

The highest preference is shown for the surface stratum in areas of cover. This is the region from which most predatory acts are originated. The second highest preference is for bottom stratum in areas of vegetation. It was noted that this habitat played an important role in allowing individuals to avoid intraspecific interactions, apparently by providing concealment. Northern pike near the substratum are seldom investigated by conspecifics, similar to the situation in juvenile atlantic salmon (Salmo salar L.) (Keenleyside and Yamamoto, 1962). Vegetated surface stratum is also preferred; the importance of this area in regard to predatory activities is stressed by Ivanova (1969). The only other preferred stratum is that of bottom areas in cover, the importance of which is probably similar to that of vegetated bottom areas. Northern pike also used vegetated and cover bottom and to a lesser extent open bottom areas for inactivity during heavy rain showers. The areas most frequently avoided are those in the open at the surface and middepth.

Benefits arising from such a pattern of habitat preferences would appear to be largely similar to those suggested for the observed habitat usage during activity periods. Concealment is important for successful predation (Ivanova, 1969; Kipling and Frost, 1970), and protection from aerial predators. Vegetation offers some structural discontinuity in the environment, which visually confines conspecifics, and thus may allow aggression to remain low. This last suggestion parallels the findings of Sale (1972).

B. Predatory Behavior

RESULTS

The most detailed description of predatory behavior in northern pike is that of Hoogland _et al_. (1956). Their description is based on observations of feeding by small northern pike (20-25 cm fork length) under laboratory conditions. The descriptions and data presented here are based on observations of larger northern pike (33-63 cm fork length) in a confined natural situation. Table 12 summarizes the standard measurements made on the fish retained for observations in 1973 and 1974.

1. Description of the Predatory Act

Hoogland _et al_. (1956) describe a predatory act for northern pike which consists of seven main components: " 1. Eye movements towards the prey, 2. Turning towards the prey, 3. Stalking, 4. Leaping, 5. Snapping, 6. Turning the prey head-forward, 7. Swallowing." Nursall (1973) combines the first three steps under the term "axial tracking".

During the present study, stalking predation, of the nature described, was observed to occur when prey were moving slowly (if injured or unaware of the predator's presence), and also when dead or artificially confined prey were presented to northern pike. If prey fled from the

Table 12. Northern pike retained in Study Stream for behavior observations 1973 and 1974, summary of standard measurements taken.

Fish	Sex	Fork Length cms	Weight gms	Remarks
1973				
MP1	female	46.5	570	escaped
JP1	male	42.2	350	collected
RT	female	46.5	530	collected
LF	male	41.5	550	escaped
UI	male	45.0	470	collected
JJP1	female	53.5	900	collected
1974				
A	female	51.4	930	died
B	male	41.5	460	escaped
C	female	55.0	1020	escaped
D	male	52.0	980	collected
E	male	50.0	880	escaped
F	male	42.0	450	collected
G	male	47.5	640	collected
H	female	57.3	1360	died
I	female	63.5	1820	collected
U	female	52.6	1110	collected
W	female	33.0	260	collected
X	female	53.5	1060	escaped
Y	female	51.5	1060	escaped
Z	female	50.0	880	collected

predator the result was a modification of steps 3, 4, and 5 of Hoogland et al. (1956), to produce what could be termed pursuit predation. Both stalking and pursuit predation began with initial detection and orientation to the prey. Following these first steps the predator may resort to either type of predation (Figure 17). It should be noted that the predatory act can be terminated at any point during its execution.

Visual detection of prey fish by northern pike was observed to occur at distances of up to four meters in open water, if the prey was moving. Due to the distance of the observer from the northern pike, during Study Stream observations, it was difficult to detect eye movements of the predator during the initial step of visual fixation of prey. This behavior was frequently observed when northern pike were approached during Scuba diving excursions. Stationary northern pike, oriented broadside to the diver, followed the passage of the observer by use of eye movements in the horizontal plane.

Orientation towards the prey occurred in two manners. Stationary northern pike orienting to slow-moving prey did so with the body held rigid, as described by Nursall (1973). This type of turning was accomplished using slight sculling movements of the posterior borders of the dorsal, anal and caudal fins, accompanied by sweeping movements of the pectoral

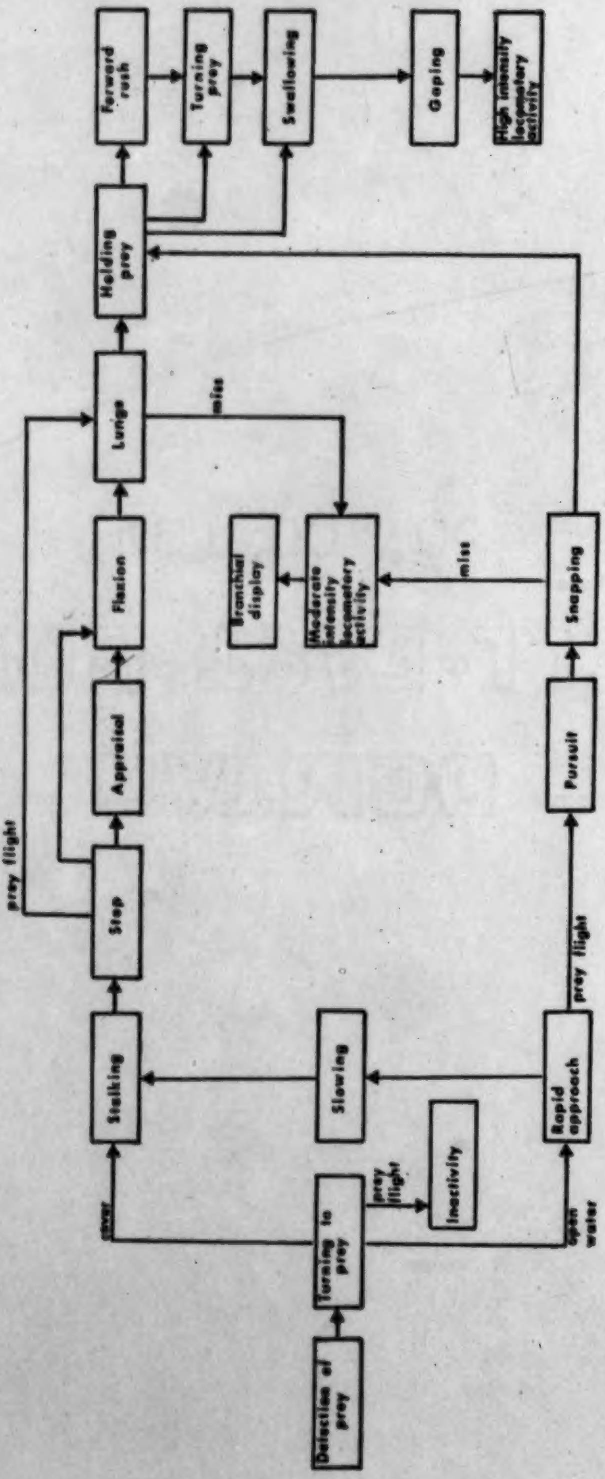

Detection of prey
Turning to prey
cover
open water
prey flight
Inactivity
Stalking
Slowing
Rapid approach
prey flight
Stop
prey flight
Appraisal
Flexion
Lunge
miss
Holding prey
Forward rush
Turning prey
Swallowing
Gaping
High intensity locomotory activity
Branchial display
Moderate intensity locomotory activity
miss
Pursuit
Snapping

Figure 17. Diagramatic model of the predatory behavior of northern pike.

fins. Eye movements occurring during the performance of such turns were observed from directly above in northern pike confined to holding tanks. As stationary northern pike executed a turn the eyes were moved synchronously at regular intervals. The eyes appeared to fix on one point and move horizontally in their sockets, to keep this point fixed, as the fish turned; when the eyes had reached the extent of their travel they flicked back to their starting positions to repeat the process. The eye on the outside of the turn was flicked ahead, and the eye on the inside of the turn was flicked backward. The second type of orientation by northern pike occurred if the prey was moving rapidly, or when the predator itself was swimming fast. This type of turn was very swift, and had the characteristics of the abrupt type of turn.

Hoogland _et al_. (1956) suggest that northern pike slowly stalk their prey from the point of initial detection. During the present study this type of approach was observed to occur if northern pike were approaching prey fish through an area of aquatic vegetation or cover. However, open water situations with slow moving or stationary prey fish frequently elicited an initial rush of moderate speed by the predator. The propulsive force in this type of approach was produced by broad, rapid sweeps of the caudal peduncle. The approach phase was the point at which stalking and pursuit predation began to diverge, with the resultant predatory strategy contingent upon the behavioral reactions of the prey fish (Figure 17).

Stalking predation

When prey fish remained relatively stationary, or if their swimming movements were slow and erratic (as with injured fish) the approaching northern pike began braking the initial rush at a distance of approximately 0.5 m from the prey. The predator advanced slowly from this point, using fine sculling motions of the pectoral and median fins. At 10 to 15 cm distance from the prey (0.25 to 0.33 the predator's body length) the northern pike stopped its forward progress, and stabilized itself with sculling movements of the pectoral and dorsal fins. In this position the prey was watched for a variable period of time. However, if the prey should attempt to flee an immediate predatory lunge usually resulted.

In cases where no escape behavior was shown by the prey, northern pike deliberately prepared for the final predatory lunge by curving the body into the characteristic 'S'-posture, described by Hoogland et al. (1956) as being "the same as the initial part of carangiform movement." The body was thus compressed and curved, with the tail at an angle to the midline (Figure 18). This posture was never held for more than one or two seconds, but Hoogland et al. (1956)

state: "If the pike's movements are hampered by water weeds however, he may stand in the 'S'-posture for some seconds." At this point the northern pike was prepared for the final lunge, with the prey lying directly ahead, usually on the same plane as the predator. The predatory lunge which ensued was produced by the violent backward thrust of the caudal peduncle, almost parallel to the midline of the long axis of the body.

The jaws of the northern pike remained closed until the last moment before the prey was struck. The jaws were then opened wide, and the floor of the buccal cavity was reflexed downwards, as described by Holler (1935). A flow of water was thus sucked into the mouth of the predator. This can be concluded, since aquatic vegetation and debris were often pulled into the mouth of the northern pike during the strike. If the prey entered the mouth of the predator the jaws were clamped shut, and held firmly closed even if the prey was only partially in the mouth.

During normal predatory attempts this sequence of events (from lunge to snap) occurred too rapidly to be clearly observed with the naked eye. However, during repeated predatory attempts, directed at prey in glass vessels, a fatiguing of the response occurred. This caused each successive lunge-snap sequence to diminish in speed and strength in relation to its antecedent. This facilitated observation of the sequence. The final capture of prey was much slower when dead prey fish were taken by northern pike, which permitted this segment of the sequence to be accurately observed.

The force of the lunge carried the head of the northern pike only about one-half a body length past the point at which the prey had been located. It appeared that the pectoral and pelvic fins were maximally extended laterally and were rotated to the vertical plane, providing the largest surface area to act as a brake to forward progress.

Pursuit predation

Pursuit predation was employed by northern pike if prey fish exhibited escape behavior while the initial predatory rush was in progress. With flight of the prey, the predator accelerated from moderate speed to near burst speed. There was a definite decrease in the amplitude and an increase in frequency of the sweeps of the caudal peduncle of the northern pike. This produced higher speed, and reduced the distance of lateral displacement of the head region in response to the tail thrusts. Burst speed swimming persisted as long as the prey fish attempted to swim directly away from the advancing predator. At a distance of from 15 to 20 cm behind the prey, the pursuing northern pike began rapidly snapping its jaws open and closed. In this case the tips of the jaws were only separated approximately two to four centimeters, where as in stalking predation the jaws were opened maximally.

Quantitative analysis - stalking and pursuit

During the course of this study 94 predatory attempts by northern pike were observed which could be classified as being of either stalking or pursuit variety. An additional 25 classifiable predatory attempts by juvenile northern pike were also recorded (Table 13). The data contained are based on attempted predation on all species of prey fish present in the observation area.

Reactions of prey fish determined the type of predation attempted. Northern pike resorted to pursuit predation in 48 (51%) of the observed attempts, and to stalking predation in 46 (49%) of the attempts. Since stalking predation frequently occurred near emergent aquatic vegetation, the outcome of these particular attempts was often obscured. In 27 cases it was impossible to determine the outcome of the stalking predatory attempts. Pursuit predation invariably occurred in open water, hence the outcome was discernible in all cases. The frequency of pursuit predation may be over estimated, since it was the more visible of the two forms.

Data suggest that stalking predation is more successful than pursuit predation (Table 13), the success rates being 22% and 10% respectively. These values were calculated assuming no success of capture in all 27 of the stalking predation attempts with obscured outcomes. Statistically,

Table 13. Success of predatory attempts observed in Study Stream during 1973 and 1974. Data include only natural encounters between northern pike and introduced prey fish. Chi square for independence used to test significance of differences.

	Adult northern pike		Juvenile northern pike	
	Pursuit Predation	Stalking Predation	Pursuit Predation	Stalking Predation
Missed Prey	43(90%)	9(78%) *+27	3(75%)	16(76%)
Caught Prey	5(10%)	10(22%)	1(25%)	5(24%)
Totals	48	46	4	21

Comparing pusuit and stalking in a 2 X 2 contingency

Adults $p>0.05$

Juveniles $p>0.05$

* Stalking predatory attempts of obscured outcome

these data do not indicate a significant difference between the success rates of the two types of predation ($p<0.15$), but if only two of the obscured attempts had been successful the difference would be significant ($p<0.05$). The probability of at least a few of the obscured attempts being successful is high on the basis of the success rate observed in the unobscured stalking attempts.

Observations of predation by juvenile northern pike indicate a greater reliance on stalking predation than that shown by adults (Table 13). The existence of incongruities between adult and juvenile predatory behaviors preclude the grouping of these data. Juvenile predatory behavior will be examined separately.

Swallowing

If a predatory attempt was successful, northern pike held the prey firmly in their jaws until struggling movements had diminished. Small prey fish were occasionally swallowed sideways by adult northern pike (also reported by Nursall (1973)). In cases where prey length was greater than the width of the predator's jaws, prey turning movements were usually employed by the northern pike.

Turning movements, used by northern pike to manipulate prey, appeared to be fairly stereotyped, and had a similar form in juveniles over two months of age and adults alike.

When the struggling movements of the prey had ceased, the predator remained inactive for a period of one to ten seconds before attempting to turn the prey. Prey was not mouthed by the northern pike, but appeared to be held firmly at all times. The predator initially flexed its head and anterior trunk to the side, at an angle to the long axis of the body. Flexion proceeded to the side which had the bulk of the prey outside of the mouth (Figure 19). The head was violently jerked back to the midline after remaining flexed to the side for only one or two seconds. The anterior portion of the predator's body did not travel across to the opposite side of the midline, but stopped abruptly as it reached the long axis of the body. This act could be repeated several times, depending upon the size and liveliness of the prey. The predator usually remained stationary while turning and swallowing prey; in some cases, especially with relatively small prey, northern pike were observed to rush forward as the prey was swallowed. Once the prey had been properly positioned in the mouth it was swallowed in one smooth motion.

Following the ingestion of prey, a variable number of mouth gapes occurred, accompanied by forward swimming. Vegetation and debris were flushed from behind the opercula with these maneuvers. During the gapes, the mouth was opened wide, while the opercula were kept closed; the mouth was then closed, and the opercula were flared open. This pattern

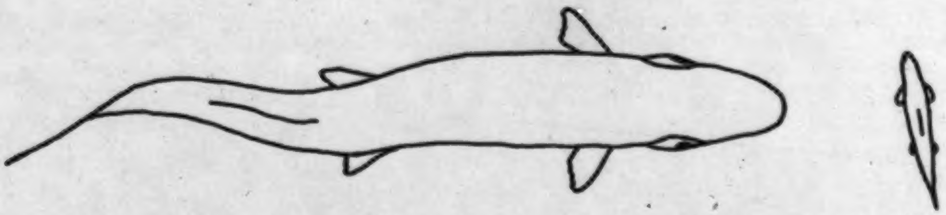


Figure 18. 'S'- posture of northern pike prior to predatory lunge in stalking predation.

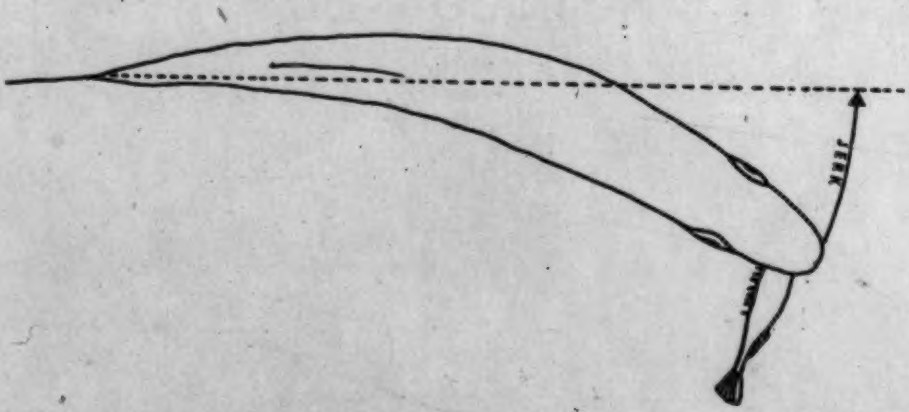


Figure 19. Body flexion of northern pike during prey-turning movements.

suggests a type of buccal pumping function similar to respiratory movements. Similar gaping movements occurred during regurgitation of partially digested fish. However, in this latter case the body of the predator was tilted forward, with the head pointing down on an angle to the horizontal. These gapes were accompanied by violent side to side shaking movements of the head, causing debris to be flushed out of the oral cavity as well as through the flared opercular region.

Data collected from stomach samples of northern pike provide indirect evidence of discriminate swallowing of certain prey species (Table 14). Walleye were swallowed head first in all cases, as were lake whitefish and burbot. White sucker and cisco were more frequently swallowed head first than tail first ($p<0.001$). Northern pike were swallowed more frequently head first, but not significantly so. This is perhaps a result of the small sample of this species examined. The three smallest forage fish, spottail shiners, trout-perch, and ninespine stickleback, were all swallowed with equal frequency in either orientation. These data suggest that northern pike selectively turn the larger prey fish before swallowing, while smaller prey fish are ingested indiscriminately.

Table 14. Direction of swallowing of prey, determined from stomach samples of northern pike 1973 and 1974. Values indicate the frequency of swallowing of each prey species head first and tail first. Total number of each prey species indicated. Effect of species of prey on direction of swallowing tested by Chi square for independence.

= approximately equal ($p>0.05$)
> greater than ($p<0.05$)
>> greater than ($p<0.01$)
>>> greater than ($p<0.001$)

Prey Species	Direction of swallowing			Total number examined
	Head first		Tail first	
Trout-perch	43%	=	57%	21
Cisco	84%	>>>	16%	19
Ninespine stickleback	66%	=	33%	15
White sucker	94%	>>>	6%	19
Lake whitefish	100%	>	0%	4
Spottail shiner	50%	=	50%	16
Northern pike	80%	=	20%	4
Walleye	100%	>>>	0%	20
Burbot	100%	>	0%	4

Color changes

On 11 separate occasions, during Study Stream observations, adult northern pike were observed to undergo rapid and distinct alterations of skin coloration and patterning. These color changes arose in association with the location and observation of prey fish. The observed changes developed during seven interactions with juvenile northern pike, two interactions with confined prey fish (trout-perch and lake chub), and two model presentations. Predatory strikes occurred only in the four artificial predatory situations. During the seven intraspecific interactions there was only observation of the potential prey by adults. The color change phenomenon was irregular in occurrence, hence its predictability was low. It was observed to develop in four different individuals over the study period.

The color change developed as an apparent lightening trend in the predominantly black dorsal region, from head to caudal peduncle. This produced a light yellow-green stripe running the length of the dorsal midline. Lightened vertical bars, intersecting the dorsal stripe, developed on the sides of the fish. There appeared to be an overall lightening in the hue of the skin, with an emphasis on the vertical zebra-stripe pattern. Areas of dark pigmentation became less obvious, giving the body an almost golden coloration. The color pattern was suggestive of that found in young northern pike.

Color change required between 30 and 90 seconds to develop fully, with decay occurring following termination of the interaction. The maximum duration of the full change observed was approximately 12 minutes. The decay process seemed to require between 10 to 15 minutes to occur. When the return to normal coloration was complete the emphasis of the vertical stripe pattern was lost.

On one occasion a normally colored northern pike moved close and stopped near a conspecific in altered color phase. This allowed accurate comparison of the two patterns, and indicated that a change had infact occurred, and that the observation was not an artifact of peculiar lighting conditions.

Post-predation behavior

Data collected during this study suggest a relationship between the outcome of a predatory act and the ensuing behavior of northern pike (Table 15). The table includes data from experimental feeding tests and excludes predatory acts with obscured outcomes.

Three different levels of locomotory activity were employed by northern pike after involvement in situations having predatory potential. Following successful predatory acts, northern pike most frequently exhibited periods of high intensity locomotor activity approaching burst speed

Table 15. Behavior of northern pike following encounters with potential prey fish in Study Stream. Data include natural predatory acts and feeding tests, but exclude acts with obscured outcome. Values indicate number of separate occasions on which specific behavior was observed to develop. Significance of differences tested with Chi square for independence.
>> indicates significantly greater than (p<0.01).
= indicates approximately equal to (p>0.05).
> indicates significantly greater than (p<0.05).

Outcome of Encounter	Inactive	High intensity locomotory activity	Moderate intensity locomotory activity	Branchio-stegal display
Successful	0	<<14(74%)>>	5(26%)	0
				∧∧
Unsuccessful	10(20%)	= 6(12%)<<	35(68%)	11(22%)
				∨∨
No predatory attempt	45(86%)	>> 0 <	7(14%)	1(2%)

Ranking of behaviors

Successful - High intensity>> Moderate>> Inactive

Unsuccessful - Moderate intensity>>Inactive = High

No predatory attempt - Inactive>> Moderate intensity = High

Ranking of display tendencies

Branchiostegal display - Unsuccessful>>No attempt=Successful

(74% occurrence). The predators swam rapidly around the area of capture. The paths followed during such activities were usually circular in shape, following the open water margins of aquatic vegetation beds surrounding the pools. The swimming speed declined gradually to normal cruising speed over a period of 2.5 to 5.0 minutes. Following the other 26% of the successful predatory acts, the predators resorted to moderate intensity locomotor activity. If predatory attempts were unsuccessful (attempts including a lunge or pursuit), the subsequent locomotor activity of northern pike was most frequently of moderate intensity (68% occurrence). In this case the swimming speed was much lower than that exhibited during the initial stages of intense locomotor activity. The return to cruising speed required less than 2.5 minutes, and the predator had often become inactive by that time. The remaining unsuccessful predatory attempts resulted in inactivity in 20% of the cases, and intense locomotor activity in only 12%. In situations where prey were observed but not reacted to, or if prey fled before a rush was initiated, the northern pike usually remained inactive (86% occurrence). Moderate intensity locomotor activity was displayed in the remaining 14% of these cases. The levels of the three activities employed were highly significantly different between the three predatory outcomes ($p<0.01$).

Branchiostegal displays were given by northern pike following 22% of the unsuccessful predatory attempts in the

1

observation channel. This only occurred once following an unutilized predatory opportunity. Displays were not observed to follow successful predation, except in the form of mouth cleaning gapes, which appeared to have a definite function. However, the intense locomotor activity following successful predation occasionally brought the predator into contact with conspecifics. In no case did the predator show an aggressive response, in fact the other individual was often stimulated to activity by the encounter.

2. Required Stimuli

Visual

The role of visual stimuli in releasing and directing northern pike predation was examined. Live prey fish were confined in glass vessels, which were then suspended in the observation channel. A total of 15 presentations, each of five minutes duration, were made. Northern pike were observed to detect the confined prey from distances as great as four meters. Predatory strikes were evoked in eight (53%) of the presentations. In a further three cases (20%) intrest was displayed by the predators in the form of approach and appraisal, but no strikes ensued. In the remaining four cases (27%) no response was observed. All of the predatory responses elicited during these tests were of the stalking-lunge variety. The northern pike approached the prey to within 10 to 15 cm, stopped, flexed, and struck. The highest number of strikes performed by one individual during a single presentation was 21. In this case the predatory response gradually declined in strength. The strikes themselves became weaker as body flexion became less and less pronounced; associated with this was an increase in the lag time between successive strikes. Lag time increased from approximately 0.5 seconds to approximately 5.0 seconds over the duration of the predatory sequence. All of the strikes elicited during these tests appeared to be as accurate as those observed in the natural situation.

Mechanical

General observations suggest the importance of mechanical stimuli in some situations as the initial indicators of prey presence. However, under natural conditions it is often difficult to separate the reactions to mechanical stimuli from those to visual or olfactory stimuli. Mechanical disturbances were produced by dropping small amounts of water (approximately 10 cc) from the observation tower onto the surface of the observation channel. Production of this type of stimulus within 15 cm of a northern pike would often result in immediate movement towards the area of disturbance. Stimuli originating behind the predator caused turning and movement towards the general area of disturbance. After initial movements the predator usually remained stationary for a short period, still facing in the direction of the disturbance. No predatory lunges ever occurred in response to the mechanical stimulus by itself.

Olfactory

To test the effect of olfactory stimuli alone, northern pike were presented with quantities of prey-conditioned water. Ten liter quantities of water were conditioned by use as a holding medium for 200 to 250 prey fish for a period of 15 to 20 minutes. The conditioned solutions were then introduced into the observation channel, by remote means, at a point two meters below the observation tower.

Eight such introductions of conditioned water were made, and in three cases northern pike moved directly through the area within a period of five minutes after introduction. In no case was an observable response elicited from the fish, but this number of tests is insufficient to clearly determine the importance of olfaction in detection of prey.

General observations were also made which pertain to the subject of olfactory stimuli. In numerous cases northern pike were observed within approximately five centimeters of dead forage fish, which were lying on the bottom or floating on the water surface. In many cases these were prey fish which had died within several minutes of being placed in the observation channel, and although inert must still have been providing some chemical substances which could have acted as olfactory cues. Northern pike never showed interest in these dead prey fish if they were stationary. However, the predators could be induced to strike and swallow dead prey fish if they were dropped onto the surface of the water and allowed to sink. When a sinking, dead prey fish fell within the field of vision of a northern pike an immediate approach usually followed. Then a period of appraisal occurred, with the stationary predator watching the prey sink. If the prey was struck, only minimal flexion was employed, resulting in a much less vigorous predatory act than those involving live prey. On several occasions the dead prey were allowed to reach the bottom before a predatory attempt took place.

Importance of prey movements

Observations of northern pike-forage fish interactions, in the observation channel, suggested that locomotory behavior of prey played an important role in releasing the predatory act (Table 16). The results include only those interactions with prey fish of acceptable size for predation, as determined from stomach samples. Moving prey fish elicited a significantly higher number of predatory responses than did stationary prey ($p<0.001$).

Fish models were employed in a series of tests to examine the importance of prey fish behavior further in relation to the predatory act of northern pike. The commercial fish model (Rapala) was presented to northern pike, in the observation area, a total of 190 times during the study (Table 17). The model was always moved through the field of vision of the predator. In the majority of cases (165) the model was pulled slowly and smoothly through the water, at a rate of approximately 0.2 m/sec, to simulate natural, slow swimming movements. In 91% of the slow swimming trials no response was exhibited by the predator, while in 7% of these trials an incomplete predatory response, in the form of orientation or short following, was elicited. A complete predatory response, up to lunge and snap stage, occurred in only 2% of the slow swimming trials. In 20 of the model presentations

Table 16. Frequency of predation by northern pike on stationary and moving, live prey fish. From total Study Stream observations 1973 and 1974. Data indicate number of cases in which specific reactions were elicited.

Reaction of Predator	Prey Activity[a] Stationary	Moving
Partial reaction	27	9
Predatory attempt	4	38

[a] Comparing effect of prey movement in a 2 X 2 contingency table $X^2 = 32.5$; $p<0.001$.

Table 17. Reactions of confined northern pike to a prey model moved at different speeds. From Study Stream tests 1973 and 1974. Data indicate number of single presentations in which specific reactions were elicited. Chi square test used.
>> greater than ($p<0.01$).
> greater than ($p<0.05$).

Reaction of Predator	Model movement pattern (approx. speed) Movement stopped* (0.5m/sec)	Slow swimming (0.2m/sec)		Fast-erratic swimming (0.5m/sec)
No reaction	0	150(91%)	>>	0
Intrest	5(100%)	11(7%)	<	5(20%)
Attack	0	4(2%)	<<	15(80%)
Totals	5	165		20

* Model movement stopped after initial fast-erratic movement had elicited following behavior.

swift and erratic movement of the stimulus object was produced by jerking it quickly through the water. In 80% of these fast swimming trials a complete predatory attempt occurred; the remaining 20% of the trials all elicited interest, in the form of short following behavior. In five additional fast swimming trials (movement stopped column) an initial following response was produced. Subsequent termination of model movement caused northern pike to stop, appraise the model for five to ten seconds, turn, and quit the area.

A series of tests was implemented to obtain information pertaining to circadian rhythms in the predatory activity of northern pike. During 398.75 hours of recording, using three types of stationary models, a total of nine predatory strikes occurred. The strikes took place in the morning (600 to 1000 hours) and evening (1630 to 2200 hours). Unfortunately, this number of responses is inadequate to allow the drawing of any definitive conclusions about feeding rhythms. The results may suggest the occurrence of negative conditioning; most of the strikes occurred shortly after the model types were changed, or after introduction of new northern pike into the observation channel. These findings are in accord with work of Beukema (1970), which indicates that under negative reward conditions northern pike can display one or two trial learning.

3. Species of Prey Fish

Behavior of northern pike in relation to species of prey was incidentally observed during general behavioral studies. Species preferences were not directly obvious from these general observations. Northern pike appeared to react in a similar manner to most species of prey fish provided. The exceptions were the reactions to spottail shiners, large walleye, and juvenile northern pike.

Spottail shiners

Adult northern pike in the observation area exhibited no particular predatory rejection of solitary spottail shiners, provided they were within the acceptable size range for predation (Table 18). However, schools of spottail shiners (minimum school size of four individuals) had a significantly lower probability of being preyed upon ($p<0.01$). In most cases, schools of this species were ignored by adult predators. In one instance a northern pike was observed to pass up an opportunity to prey on five, 7.5 cm spottail shiners in a school, and then attempt to capture a solitary, 7.0 cm lake chub 70 seconds later. These findings are substantiated by Scuba diving observations of analogous encounters between northern pike and spottail shiner schools in natural littoral areas. In 29 cases spottail shiner schools were observed to pass within sight range of northern pike, yet no predatory attempts resulted. Stomach samples from

Table 18. Results of observed interactions between northern pike and spottail shiners, solitary and in schools. From Study Stream observations 1973 and 1974.

Reaction of Predator	Prey Group[a]	
	Schooling*	Solitary
Interest	2	11
No Interest	16	8

* Minimum school size observed was 4 individuals

[a] Comparing effect of schooling on predator reaction with effect of solitary prey, in a 2 X 2 contingency table $X^2 = 6.9$; $p<0.01$.

northern pike also indicate that spottail shiners were consumed less frequently than would have been expected on the basis of the relative abundance of this prey species (Figure 13).

In an effort to further explore the problem of the low predation on abundant spottail shiners, a special examination of that prey species was conducted. Nursall (1973) states that spottail shiners may enjoy a degree of protection from predation by northern pike; this apparently results from the difficulties encountered by a solitary predator attacking schooling prey fish. He reports the use of a protean defence tactic (see Humphries and Driver (1970)) by spottail shiner schools when attacked by northern pike. During Scuba diving observations it was found that spottail shiner schools would approach a stationary, underwater observer to within 0.5 m. A sudden hand movement toward the school produced the flash expansion behavior described by Nursall (1973). This presented an extremely confusing array of visual stimuli. Attempts to follow the progress of a single fish were hampered by continual, abrupt, and unpredictable directional changes made by individuals, and associated changes in total school morphology. This phenomenon had the attributes of a scatter display (Humphries and Driver, 1970), the effectiveness of which depended upon the appropriate response of all school members.

Information from stomach samples of northern pike provides further evidence indicating the predation reducing attributes of schooling behavior of spottail shiners. A small portion of the spottail shiner population in Kakisa Lake was infected with the cestode parasite Ligula intestinalis. This parasite resides in the abdominal cavity of the host, causing marked distention of the abdominal region in extreme cases. Observations of infected spottail shiners indicated that swimming ability was impaired, which resulted in a sluggishness of response to coordinated school movements. Generally, it appeared that the infected fish had to swim harder than normal individuals to remain with the school. On the basis of the findings of Humphries and Driver (1970) and Nursall (1973), it was postulated that northern pike might selectively prey upon those spottail shiners showing discordant schooling behavior. To test this theory the incidence of parasitized spottail shiners in the stomachs of northern pike was compared with the incidence of parasitized spottail shiners in the general lake population.

Northern pike in Kakisa Lake consumed parasitized spottail shiners six times more frequently than would be expected if predation on this species was random ($p<0.05$) (Table 19). Ligula intestinalis from spottail shiners in northern pike stomachs were two to three times heavier, in relation to host weight, than parasites from spottail shiners in the lake population (Table 19). However, a portion of this

Table 19. Occurrence of Spottail shiner infected with *Ligula intestinalis*, in the stomachs of northern pike and in samples from the lake population. Data from 1973 and 1974.

	Spottail shiners from the stomachs of northern pike	Spottail shiners seined from the lake population
Number examined	23	71
Number infected with *Ligula intestinalis*	4	2
Percent infected	17.4	2.8
Average weight of parasite as percent of host weight	23.7	8.5

$$\text{Index of selectivity} = \frac{\text{Percent occurrence in food}}{\text{Percent occurrence in population}} = \frac{17.4}{2.8} = \underline{6.2}$$

weight difference may have arisen from a slight reduction in weight of the consumed spottail shiners, caused by the digestive processes of the northern pike.

Adult walleye

Data collected from stomach samples and direct observations indicated that northern pike were capable of capturing and consuming walleye less than 0.33 the body length of the predator. Observations of predatory attempts on larger walleye, up to 0.50 the body length of the predator, suggested that northern pike exercised discrimination in the capture of these individuals.

Four extended interactions between walleye of 20 to 22 cm fork length and northern pike (50, 52, and 41 cm fork length) were observed. In all cases the nature of the interaction was similar. A walleye moving through the open water of the observation channel elicited an immediate following response from any adult northern pike within sight range. The walleye, detecting pursuit by the predator, reacted by erecting its paired and median fins. It continued to move forward more slowly and awkwardly, propelled by high amplitude sweeps of the caudal peduncle, its progress being impeded somewhat by the extended paired fins. Forward progress of the walleye continued until the northern pike had closed to approximately one meter. The approach by the predator was not a dash, but rather accelerated swimming of adequate velocity to overtake the prey. As the northern pike moved within one meter, the walleye veered away on a right angle to its original direction of travel. This maneuver caused the predator to slow and execute a turn to follow movements of the prey. The walleye reacted by further course adjustments to direct its path of travel around the predator, along the perimeter of a circle with the northern pike at its center. The prey dropped approximately 10 cm deeper in the water, and tilted its dorsal surface towards the predator at approximately 45° from the vertical. This action presented the erected dorsal spines of the walleye directly to the predator. The northern pike was stationary during this phase, only performing turning movements to follow visually the progress of the circling walleye. This activity continued, with the walleye making four or five complete circles, until the predator turned and departed. When this occurred the walleye proceeded on a tangent to its circle of travel, in the opposite direction to that taken by the predator. While leaving the area of encounter, the slowly departing walleye kept its fins erect. The total duration of the activity sequence was approximately 50 to 70 seconds.

In none of these interactions were northern pike ever observed to direct a strike at the walleye being followed. The sizes of the prey were near the acceptable limits for predation as suggested by Hoogland et al. (1956), but were slightly higher than those suggested by Nursall (1973).

Cannibalism

From stomach samples it was evident that in Kakisa Lake northern pike are cannibalistic. Numerous cannibalistic acts were also noted in the observation area population. The nature of the behavior of predator and prey in these interactions was somewhat different than in encounters between adult northern pike and other species of forage fish. During the study 35 interactions between adult and juvenile northern pike were observed. The outcome of these interactions varied, depending upon the specific situation. In 30 of the 35 interactions adults were aware of the presence of the smaller conspecifics, hence only in these 30 cases was there potential for predatory acts. In 30% of these 30 interactions adults exhibited no specific interest in the prey-sized northern pike. In a further 30% the adults showed interest by orienting to the juveniles. In an additional 23% of the cases adults showed heightened interest by carrying out initial movements toward the prey. Only five (17%) of the 30 interactions resulted in the execution of a complete predatory attempt (three pursuit and two stalking). None of the observed attempts was successful. Adults often terminated the activity immediately upon the occurrence of escape attempts by juveniles.

The nature of adult-juvenile northern pike interactions appeared to be controlled, to a large extent, by the repertoire of behaviors employed by juveniles during interactions.

1. Juveniles tended to avoid adult northern pike. In general, juveniles spent much time in very shallow water along the shoreline areas, virtually out of reach to adults. In addition to habitat selection, juveniles exhibited actual avoidance behaviors, which tended to reduce the frequency of intraspecific encounters. Juveniles moving along the vegetation beds, in the observation channel, would usually stop immediately upon sighting an adult northern pike at distances up to 3.5 m away. Even if adults were inactive and facing in the opposite direction the juveniles would react. The small northern pike would then back up for a short distance, while still facing the adult. At a variable distance from the adult the juvenile would turn, and move away from the area at a moderate speed. 2. Juvenile northern pike reacted, almost immediately, to any orientation or overt intention movements directed towards them by an adult. There was a 78% occurrence of flight by juveniles which adults were orienting towards. The usual response of the juvenile was to move quickly to an area of aquatic vegetation.

3. Juvenile northern pike, when fleeing from an adult, resorted to the use of extremely confusing protean escape behaviors. These usually involved a series of rapid leaps along the surface of the water, the effect produced being somewhat akin to that of a flat rock skipped across the water surface. The last splash was followed by a dart underwater, usually at an angle to the initial direction of travel, terminated by an abrupt stop, often in an area of aquatic vegetation.

4. If a juvenile northern pike found itself being examined at close range by an adult, a special type of behavior, not observed in any other forage species, was employed. The juvenile turned to face directly toward the adult, then very slowly began to back away towards an area of aquatic vegetation. As the adult entered the vegetation, the juvenile darted quickly to the side, and escaped through the cover.

4. Social Facilitation in Predation

Northern pike appeared to react to conspecifics seen carrying out pursuit predation. In 20 of the observed pursuit variety predatory acts, other northern pike were present in the area, and thus could observe the predatory attempt. In 11 of the 20 cases (55%), the second fish reacted positively to the actions of the predator. These positive reactions consisted of high intensity locomotor activities directed toward the predator, or along an arc around the area of predation. In the remaining 9 cases (45%) the second northern pike did not react to the activity of the first. Of 1120 observed interactions between northern pike, occurring in the absence of predation, only 193 resulted in a following response by one individual. This level of cohesive responses was significantly lower than that observed during interactions following predation ($p<0.001$). The outcome of the initial predatory attempt did not seem to dictate the nature of reactions exhibited by the second fish. The second northern pike may, infact, become active before the initial predatory attempt had terminated. Stalking predation tended to occur hidden by vegetation, and was of short duration; the act was seldom observed by other northern pike, and never reacted to.

5. Predatory Behavior of Juvenile Northern Pike

During observations, on the Study Stream, a number of predatory acts by young of the year northern pike were observed and recorded. These observations indicate the existence of certain differences between the feeding behavior of juveniles and adults. The juvenile northern pike were between five and eight centimeters in fork length; the prey fish were spottail shiners and white suckers between two and three centimeters in fork length.

Juvenile northern pike were seldom seen in open water except during predatory forays. They rushed at the prey fish from hides in aquatic vegetation beds. The initial rush was similar to that used by adult northern pike. It could be followed by a stop and appraisal of the prey, or less frequently by a continued predatory rush directly to the prey. This continued predatory rush was similar to the pursuit situation in adult predation, except that the prey of juveniles seldom reacted by fleeing. The general behavior of the prey was dissimilar to that of adults of the same species. The small spottail shiners and white suckers did travel in loose schools, but rarely displayed the antipredator behaviors used by adults of the species. The small forage fish only swam slowly away from the point of disturbance created by a predatory act. No flash expansion (Nursall, 1973) of schools of juvenile spottail shiners occurred in response to the attacks of predators. It appeared that spottail shiners developed escape behaviors as their locomotory ability improved, and after a number of encounters with predators.

Stalking-type predation was the form most commonly used by juvenile northern pike (Table 13). The young predators, in some cases, would follow the schools of prey, and periodically lunge at peripheral individuals. Juvenile northern pike were also able to move into prey schools, hang motionless, and strike repeatedly at individuals within range. The situation faced by juvenile northern pike appeared to be more conducive to accurate predatory strikes than that faced by adults. Yet the success rate of juvenile predation was only 24%. The general impression was that young northern pike had not yet gained the skill achieved by adults, but the naivete of the young prey fish allowed a comperable predatory success rate to exist.

DISCUSSION

1. Description of Predatory Act

Descriptions of the predatory act of northern pike have been given by Hoogland et al. (1956) and Nursall (1973); these descriptions are largely consistent with the sequence of behaviors observed in the stalking form of predation. The pattern of action employed in this form of predation is apparently a stereotypic trait of the species. The sequence, never-the-less, can not be termed a fixed action pattern, since its form is not independant of environmental stimuli (a criterion of Hinde (1966)). The act can be terminated at any point in its execution (Hoogland et al., 1956), and the individual steps can be modified by specific attributes or behaviors of the prey organism (Figure 17).

The initial detection and orientation components of the predatory act are similar to those reported by previous workers. The slow stalking approach phase, outlined by Hoogland et al. (1956), was observed during the present study only when northern pike were moving through aquatic vegetation towards a prey organism. In open water the predator's initial approach was more rapid than that previously described. This difference in observations may arise as a result of a slight modification of approach behavior employed by northern pike when confined in small holding systems, such as the aquaria used by Hoogland et al. (1956). The effects of confinement may also explain the failure of northern pike to display both stalking and pursuit predation during previous behavioral studies. The approach phase is the initial point at which the divergence between stalking and pursuit predation is manifest (Figure 17).

Stalking predation

At a distance of approximately 0.5 m from a stationary prey the predator checks its initial rush, and begins stalking slowly forward. At this point the behavior again conforms to that described by Hoogland et al. (1956). The subsequent cessation of movement by the northern pike, and appraisal of prey for a period of variable length is consistent with the findings of Nursall (1973). On the basis of the rejection of stationary prey models (Table 17, Movement stopped column), it is evident that northern pike do assess the acceptability of prey organisms during the appraisal phase. During this phase, slight movements by the prey, which could represent intention of escape, often act as stimuli triggering an immediate predatory lunge. In some instances it appears that these stimuli are of sufficient magnitude to override inhibitions which might normally prevent predation on certain types of prey. This is suggested from pilot tests conducted with prey models. Northern pike would appraise, but not strike at a model which had ceased moving. In a small portion of the pilot tests, northern pike were induced to strike, after a three to five second period of appraisal, by imparting movement to the model. A similar reaction to prey movement is shown by juvenile yellow-bellied racers (Coluber constrictor) (Herzog et al., 1974). This snake will temporarily terminate pursuit of prey which cease moving, but will strike immediately upon resumption of prey movement. Hoogland et al. (1956) note that ninespine sticklebacks occasionally escape northern pike predation by remaining motionless. In situations with acceptable live fish, no prey movement is necessarily required to induce northern pike to assume the 'S'- posture after a period of appraisal. This fact was initially reported by Nursall (1973), who noted that the situation is in contrast to that suggested by Baerends (1957).

The 'S'- posture, assumed prior to the final predatory lunge, brings the caudal fin away from the body midline and forward. The result is similar to the shortening in length of a coil spring being compressed upon itself. As a consequence, the subsequent thrust of the caudal fin appears to be directed backward closer to the parallel of the long axis of the body than is the case in normal swimming movements. One advantage of such a posture is the reduction in sympathetic, lateral head displacement in response to the caudal thrust. If the predator's head was laterally displaced, as from a normal side to side caudal movement, it might be expected that compensatory aiming would be required. Then it would be necessary for the predator to face to one side of the midpoint of the prey's body. All observations indicate that northern pike face directly towards the prey prior to a predatory lunge. This is consistent with the findings of Nursall (1973), who states that during predation northern pike orient their body "so that the long axis points directly towards the prey."

The predator's mouth remains closed until the last instant before the prey is struck. This habit would appear to be functional in two respects. First, by keeping the jaws closed the predator minimizes the surface area of its leading edge, which allows the snout to act as a shearing surface producing a minimal pressure wave in the medium ahead. A larger leading edge would increase the size of the pressure wave (Gosline, 1971), which could push a small prey ahead of the predator, plus act as a mechanical stimulus eliciting prey flight. Second, Hoogland *et al*. (1956) state that the rapid mouth opening causes a flow of water to move into the buccal cavity of the predator. It seems plausible that this flow could function to pull a small prey organism into the mouth of a northern pike.

Pursuit predation

Pursuit predation appears to develop only in situations which allow predators and prey fish to swim rapidly for distances of at least three to four meters without having their progress impeded by physical barriers. Agreement between present findings and those of Ivanova (1969) is apparent, since she states that in the wild northern pike frequently pursue their prey.

Escape-fleeing of prey fish seems to be the only stimulus required to induce a conversion from stalking to pursuit predation. Acceleration to burst speed enables the northern pike to overtake most prey fish which flee directly away from the predator. The rapid snapping movements of the jaws, associated with overtaking of prey, do not seem to be as perfectly coordinated with initial contact as the single snap used in stalking predation. Repeated snapping apparently functions more in the nature of trial and error. The small distance which the jaws are opened during snapping likely minimizes the perturbations of laminar flow of water over the predator's body, and thus minimizes the turbulence drag created. If the mouth was held open wide, without snapping, drag forces would be greatly increased resulting in a reduction of pursuit speed.

Comparison of pursuit and stalking predation

These two types of predation are well adapted for the situations in which they occur. In pursuit predation northern pike can and must direct their attempt along the path to which the fleeing prey fish has committed itself. An increase of predator speed is logically necessary to allow overtaking of the prey. The appraisal phase is eliminated in this case, but it may be suggested that a fleeing prey under normal conditions is usually an acceptable one. In stalking predation, in open water, the initial approach speed is reduced as the predator draws near a nonfleeing prey. In this situation the prey has not committed itself to any direction of movement, and retains the option of flight in a variety of directions. A northern pike approaching at high speed would appear to have a reduced ability to make compensatory course adjustments, should the prey fish move just prior to contact. Slowing the approach should increase the angular mobility of the predator, and also allow appraisal of the prey. The suddenness and shortness of the final lunge would reduce the chances of missing the prey organism.

Quantitative aspects of stalking and pursuit predation

Predatory acts comprised approximately 50% stalking and 50% pursuit behavior. Because of the importance of prey behavior in determining the mode of predation employed, it is not possible to suggest that similar frequencies would exist in wild populations.

The success rate of stalking predation, including the 27 obscured attempts as failures, was twice that of pursuit predation (Table 13). Nursall's (1973) value of 41% success of stalking predation implies that the 22% success rate observed in the present study is perhaps an underestimate. It seems that the ratio of 10 successes to 9 failures (53% success) in only the 19 unobscured attempts is a better estimate of the actual level of success, than when the obscured attempts are included. The revised value indicates even more strongly that northern pike, of the size range used, are best adapted to the use of sudden, straight line predatory strikes. This can also be concluded from the general external morphology of this predator. Lagler et al. (1962) and Gosline (1971) suggest that fish with elongate bodies and posteriorly placed dorsal fins are well adapted for speed, and less so for executing tight turns. The occurrence of stalking predation largely depends upon a lack of prey flight, which is insured if the predator strikes from areas of cover or vegetation. This fact, coupled with the higher success rate of stalking predation, indicates the critical importance of aquatic vegetation for the existence of northern pike.

Swallowing

The stereotyped nature of prey-swallowing movements employed by northern pike, and their similarity in juveniles and adults alike, indicates that this behavior originates largely as an innate pattern. These movements are not, apparently, completely immune to a degree of modification through experience, since Hoogland _et al_. (1956) find starved northern pike to become more proficient at swallowing _Gasterosteus_ with repetition of the act.

Head movements utilized by northern pike, while manipulating prey, imply that the inertia of the prey's own body is responsible for causing it to turn. The predator's head is flexed sideways and returned sharply to the midline, where it abruptly stops. Mouth pressure must be slightly reduced at this point, since the prey's body turns in the predator's jaws as the abrupt stop occurs. Hoogland _et al_. (1956) state, and present findings agree, that prey are not mouthed during the swallowing process. Once correctly positioned, prey are ingested smoothly, with associated jaw movements absent. Wunder (1927) postulates that this process is mediated by movements of the tongue on the floor of the mouth. Gaping movements invariably follow the disappearance of the prey into the buccal cavity of the predator. Hoogland _et al_. (1956) assume that gaping functions in completing the ingestive process, and also in cleaning the buccal region. Observations, of scales and pieces of vegetation being flushed from the opercular region during gaping, support the second assumption of Hoogland _et al_. (1956).

Large prey fish are regularly ingested head first by northern pike (Table 14). Swallowing of large prey fish in this orientation should have several advantages. Firstly, the head of all prey fish is somewhat pointed, while the tail is flexible and expandable. The relative merits of directing a solid, pointed object into the esophagus over the disadvantages of directing a flexible, expandable object are obvious. Secondly, most prey species are covered with tough, caudally directed scales. Ingestion of prey anterior end foremost would allow interlocking of the caudally directed teeth on the tongue of the predator with the free edges of the prey's scales. Such a purchase would facilitate forcing large prey into the constricted esophagus. Thirdly, the dorsal spines of walleye can only be depressed against the body by a caudally directed force. This feature appears to preclude any tendency of northern pike to swallow individuals of this species tail first (Table 14).

Smaller prey fish are swallowed with approximately equal frequency head and tail first. The small relative size of these fish apparently makes tail first ingestion possible. Nursall (1973) documents a case of a spottail shiner being swallowed sideways by a northern pike. Hoogland _et al_. (1956) and Roberts (1975) agree that the spines of ninespine stickleback offer little deterrent to northern pike predation. Present findings substantiate this suggestion, by illustrating that this prey is not swallowed head first significantly more often than tail first (Table 14).

Color changes

In 11 cases, which all possessed the attributes of predatory situations, northern pike were observed to undergo distinct changes in color pattern and general body hue. Baerends *et al*. (1955) report color changes in *Lebistes reticulatus* occurring over a period of several minutes or less. These authors conclude, from the time required, that the changes are under nervous rather than hormonal control. The period required for color change in northern pike is approximately 30 to 90 seconds, implying that nervous control is likely involved in this species also. Color changes in *Lebistes reticulatus* (Baerends *et al*., 1955) and *Salmo salar* (Keenleyside and Yamamoto, 1962) were associated with courtship and agonistic activities respectively. Baerends *et al*. (1955) and Hinde (1966) indicate that in many cases alteration of external coloration reflects changes in motivational state. In northern pike the changes were in all cases coincident with prolonged appraisal of prey fish. It seems that the color changes observed may indicate a change in predatory motivation. Since few complete predatory responses were associated with color changes, it could be assumed that the change in motivational state results from conflicting drives for and against a predatory response. The irregular and infrequent occurrence of color changes suggest that the phenomenon may only develop under specific conditions, which partially depend on the abnormality of the stimuli, causing inhibition of a normal response.

2. Post-predatory Behavior

The intensity of locomotory activity undertaken by northern pike subsequent to encountering a potential prey organism is contingent upon the result of that encounter. Following a successful predatory act northern pike tend to employ high intensity locomotory behavior for travel in the general area surrounding the point of capture. The predator appears to engage in intensified searching activity. This suggestion is consistent with findings of Tinbergen et al. (1967). They state that carrion crows (Corvus corone) exhibit intensified "area restricted searching" following the discovery and consumption of a prey item. Threespine sticklebacks will also intensify searching on a restricted area of the substrate around the point of prey capture (Thomas, 1974). Both of these studies find that the level of locomotor activity is reduced, and the path of travel becomes more tortuous during area restricted searching. This is not inconsistent with present findings, since in the studies of Tinbergen et al. (1967) and Thomas (1974) the prey organisms were sedentary and partially camouflaged. A predator searching for a sedentary prey will intensify its quest by becoming more meticulous, and thus reduce its speed of travel. Following successful predation northern pike activity is increased, but travel is confined to the general area by following arcs around the point of capture. The prey in this case are mobile, and survivors tend to scatter away from the point of attack. Hence the predator patrolling for remaining prey organisms must search over a larger area. An increase in locomotory activity may be necessary to cover the immediate region before other prey have fled far from the area.

The impetus for intensified searching seems to arise from a heightened predatory drive in a still unsatiated predator. It is assumed that the response is functional if it increases the efficiency of the predator in encountering additional prey items. Thomas (1974) notes that the response is only effective if the distribution of the prey species is such that the probability of discovering a second prey item is greater near to, rather than far from, the first prey item.

Following unsuccessful predatory attempts the subsequent locomotory activity levels tend to be consistently lower, and the duration shorter, than activity following successful acts (Table 15). The paths of travel are not closely confined to the area of the attempt, and appear to lack a definite pattern. In 20% of the unsuccessful attempts no subsequent activity was undertaken, while this was never the case when attempts were successful. These findings lend support to the suggestion that the outcome of the initial attempt has a controlling influence on the level of predatory drive. Displays were given by northern pike significantly more often following unsuccessful attempts than in either of the other two cases (Table 15). Tinbergen (1952) indicates that the occurrence of apparently irrelevant behavior following an unsuccessful consummatory act may reflect thwarting of a specific drive. Based on the findings of McFarland (1965), it seems that the displaying may represent a displacement activity. Displacement activities, such as this, can function in the release of excess impulses, when inhibitions prevent their release through normal channels (Tinbergen, 1952). The theory indicates how the displacement activity could arise, but it does not suggest the functional significance of an inhibition of high intensity locomotory activity when predatory attempts fail. One possible value of an inhibition of further searching can be proposed. If the lack of predatory success experienced were due to the inherent ability of the particular prey species to avoid predation, then the probability of capturing any individual of that species would be low. It would then not be energetically expedient for the predator to intensively search the immediate area, even if other individuals of that species were present. The reactions of northern pike to schools of spottail shiners, encountered in open water, seem to support this suggestion. This pattern of behavior is consistent with suggestions of Schoener (1969), who proposes that for optimal efficiency, predators must strive to minimize either pursuit or searching time.

When northern pike detect prey but do not attempt to capture it, there is a tendency for the predator to remain inactive. The phenomenon of prey rejection has been discussed by Thomas (1974). He finds that rejection of prey induces "changes which are antipodal to those of discovery resulting in eating." For threespine stickleback this entails an initial decrease in searching intensity and movement away from the site, which has been termed "area avoided searching" by Tinbergen _et_ _al_. (1967). It might be expected that the reaction of northern pike would be somewhat different, since this predator often hunts by remaining stationary, and reacting to prey moving by. Thus it does not necessarily follow that this predator would quit the area if a prey item was not acceptable. However, data collected in a seminatural situation do not lend themselves well to analysis of this particular aspect of predatory behavior. It is not known whether the failure to react is caused by actual rejection of the prey, or if general predatory drive is low at the time, in which case any prey would fail to elicit a response. Experiments conducted under controlled conditions are required to justify further comment on this topic.

3. Predatory Stimuli

Previous studies are not in complete agreement as to which sensory modalities are of primary importance in the predatory act of northern pike. Solman (1945), Hoogland *et al*. (1956), and Coble (1973) indicate that visual stimuli are involved in the directing and releasing of a predatory act. Wunder (1927) and Nikolsky (1963) contend that the lateral line is the main sensory system mediating orientation and release of a predatory act, while the eyes only function in compensation during the lunge. McNamara (1937) has proposed that olfaction is of importance to northern pike. Results of the present study indicate that all of these sensory modalities can be employed by northern pike during predatory activities, but that relative importance of each modality can vary with the situation.

Prey fish confined in glass vessels were presented to northern pike to provide visual stimuli only. In the waters of the Study Stream, visual stimuli were sufficient to attract predators from distances up to four meters away. This is a slightly greater maximum reaction distance than the 0.6 to 2.4 m maximum determined by Solman (1945) for clear waters. Visual stimuli alone were also sufficient to elicit "S"-posture, and release predatory lunges. All strikes released by visual stimuli alone were as accurate as those directed at unconfined prey during stalking predation.

A further indication of the importance of visual stimuli is gained from the fact that northern pike would repeatedly consume dead prey fish, which had been placed on the water surface, and were in the process of sinking. This is in contrast to statements of Frost and Kipling (1967) that northern pike will not consume inert prey, even if it is moved by water currents. However, their studies were conducted in the laboratory, which perhaps modified the predator's feeding behavior, as found by Beyerle and Williams (1968). Thus it is evident that visual cues alone can account for detection, orientation, and the release of accurate strikes at prey fish.

Wunder (1927) and Nikolsky (1963) base their assumptions on observations of successful predatory acts by blinded northern pike. By removing the predator's ability to visually detect prey, these workers determined that mechanical stimuli alone will elicit orientation and the release of predatory lunges. Although this type of experimental manipulation makes possible determination of the existence of a specific sense, it is somewhat misleading, since it deprives the animal of a normally present sensory modality. By dropping small amounts of water onto the surface of the study stream, mechanical stimuli alone were presented to the predators. These stimuli, occurring within 15 cm of northern pike, elicited accurate orientation and initial approach toward the point of disturbance. This response could be elicited by stimuli emanating from any point in front, behind, or lateral to the predator, suggesting detection by mechano-receptors. The complete failure of these fish to direct predatory lunges at points of mechanical stimulus indicates that the absence of visual cues, in a situation where they would be normally present, inhibit the performance of a complete act. The findings of Wunder (1927) and Nikolsky (1963) are not without some support, since Mauck and Coble (1971) find that northern pike continue to feed on live prey fish even when turbidity levels are high enough to preclude visual detection of prey. Apparently, in cases where the sense of vision is naturally impaired, mechanical stimuli are utilized to direct and also release predatory acts.

Olfactory stimuli seem to play a minor role in orienting or releasing the predatory act of northern pike in clear water. Northern pike would not react to solutions of prey-conditioned water placed in the observation channel, nor would they consume dead prey fish which were stationary. These findings are based on the reactions of northern pike in clear water. Under extremely turbid conditions and during the hours of dusk northern pike will consume stationary, dead prey fish, which are lying on the substratum (personal observations, Red Deer River). Presumably, olfactory cues allow detection and orientation of northern pike to these inert prey.

Data indicate that at distances of greater than approximately 15 cm detection of prey is based on visual stimuli alone, as suggested by Hoogland _et al_. (1956). Visual and mechanical stimuli function in orienting northern pike to prey in clear water, but mechanical stimuli are only important at close range. Appropriate visual stimuli control the release of predatory lunges in clear water. When visual cues are eliminated by turbidity or darkness, northern pike can detect and capture prey by employing mechanical or olfactory receptor systems. This plurality of prey detection systems would appear to have extreme functional importance to a piscivore frequently subjected to sudden and prolonged periods of turbid water conditions.

Prey movement

The studies of Hoogland *et al*. (1956), Baerends (1957), Beyerle and Williams (1968), and Mauck and Coble (1971) collectively suggest that prey movement is important in eliciting the predatory act of northern pike. Data obtained during the present study statistically substantiate these suggestions (Table 16). Results of prey-model presentation tests indicate that not only movement but type of movement effects the responsiveness of northern pike to potential prey fish (Table 17). The low responsiveness of northern pike in slow swimming trials indicates that the stimulus configuration of the model was deficient in some respect. The predators displayed significantly higher responsiveness to the same model when speed and irregularity of movement were increased. It seems plausible that rapid movements of a prey provide a stronger total visual stimulus, by increasing the number and variety of aspects in which the prey is viewed. The increased rate at which these visual stimuli are received by the predator could, through heterogeneous summation, compensate for any deficiencies inherent in the stimulus configuration of the model. Hinde (1966) reports that the pursuit response of the male fritillary butterfly (*Argynnis paphia*) is dependent on speed of model movement, color, and distance for its elicitation. He notes that increasing the speed and manner of model movement can compensate for its other character deficiencies, and thereby elicit a pursuit response. This situation, which Hinde (1966) attributes to stimulus summation, is basically similar in its motivational properties to the presentation of prey models to northern pike. In no case did northern pike fail to show a reaction to the fast moving model, while this was the most common result of slow swimming trials. This fact seems to negate the possibility that the only effect of fast swimming was an obscurement of the model's deficiencies.

In the wild this type of response by a predator may be adaptively significant, if prey displaying abnormal swimming behavior possess an impaired ability to escape predation. The studies of Beyerle and Williams (1968) indicate that the erratic behavior of newly introduced prey increases their vulnerability to predation by northern pike held in aquaria.

4. Prey Species

Observations indicate that the predatory reaction of northern pike is essentially similar for most species of prey provided. Mauck and Coble (1971), using other species of prey fish, report similar findings. The exceptions in the present study are the special reactions of northern pike to spottail shiners, large walleye, and juvenile northern pike. Results indicate that the unique behaviors of these prey provide the impetus for a modification of behavior of the predator.

Spottail shiner

The schooling behavior of spottail shiners was found to reduce their accessibility to northern pike, as suggested by Nursall (1973). Conversely, Beyerle and Williams (1968) state that schooling increased the accessibility of certain prey species to northern pike. Descriptions given by Beyerle and Williams (1968) strongly suggest that the prey behavior they observed was not schooling, as defined by Keenleyside (1955), but rather nonpolarized, facultative aggregating. This distinction is critical in the light of the predation reducing attributes of coordinated schooling behaviors (Breder, 1967; Seghers, 1974) compared to the predation enhancing attributes of aggregations (Ivanova, 1969). Northern pike are significantly more responsive to solitary spottail shiners than to schooling groups (Table 18). This indicates that the attributes of the school, and not the species per se, have an inhibitory effect on the predatory tendencies of northern pike. Additional evidence, substantiating the importance of schooling as a defence against predation, is contained in the work of Seghers (1974). He examined the schooling behaviors of populations of Poecila reticulata in the wild. In populations having few fish predators, schooling is poorly developed or absent, while populations with abundant fish predators show highly developed schooling tendencies.

Humphries and Driver (1970) discuss the theoretical basis for the effectiveness of integrated schooling behavior as a defence against predation. They suggest that the explosion of the prey group, when attacked, presents a myriad of visual stimuli, as the individual members flee in various directions. These stimuli apparently arouse, in the predator, a number of incongruous orienting responses, which conflict with one another causing a decrease in efficiency of the predatory response. For efficient predation it seems imperative for northern pike to orient accurately toward a single individual, and then carry out a very precise and well timed act. Nursall (1973) describes this by suggesting that the predatory movements of northern pike have an almost mechanical appearance.

Functionally, it would be energetically expensive for these predators to repeatedly attempt capture of normal spottail shiners from a school. Presumably, repeated unsuccessful attempts to capture this prey from a school could act as negative rewards to the predator. Beukema (1970) finds that northern pike can undergo negative conditioning, in relation to predation on lures, by one or two trial learning. In light of present observations Beukema's (1970) work supports the assumption that northern pike do learn to partially abstain from attempts to capture normal spottail shiners from schools.

The disproportionate use of parasitized spottail shiners (Table 19) lends additional support to the assumption that the integrated behavior of school members, and not a repulsive characteristic of the species itself, is responsible for lowering the responsiveness of northern pike to this prey. Heavily parasitized spottail shiners display movements which are not in harmony with those of the general school. These particular individuals attract one's attention, and are easier to visually isolate than other school members. The errant behavior of the parasitized prey fish within the school may be detectable to the predator, causing a rise in the normally low responsiveness of northern pike to schooling spottail shiners. The bias toward exploiting prey of low fitness is consistent with optimal predatory strategy (Slobodkin, 1968). Hertig and Witt (1969) report a similar situation. They find small, largemouth bass (*Micropterus salmoides*) infected with trematodes, *Dactylogyrus*, to be more vulnerable than controls to predation by bowfin (*Amia calva*). Mauck and Coble (1971) note that disease increases the vulnerability of prey fish to predation by northern pike.

Adult walleye

Interactions with adult walleye provide the strongest evidence indicating the ability of northern pike to visually recognise different prey species. Northern pike appear to show a recognition of walleye from the outset of an interaction. This is indicated by the manner in which adult individuals of this prey species are approached by the predator. With walleye, the approach is only of sufficient speed to overtake the prey, while with other northern pike or white suckers, of approximately the same size as a walleye, the approach is a rapid predatory rush. Hoogland *et al*. (1956) document visual rejection of ninespine stickleback by experienced northern pike. They conclude that the unique movement pattern of this prey is likely the characteristic which acts as a cue to the predator.

The behavior of walleye pursued by northern pike is unique among the prey species examined. Northern pike could likely overtake a fleeing walleye, and possibly obtain an effective grasp on the caudal portion of the prey's body. This opportunity was not presented to northern pike during observations, since the walleye did not flee from the predator. Rather, this prey assumes a defensive posture, apparently depending upon its substantial armament to deter a predatory attempt. Green sunfish (*Lepomis cyanellus*) and largemouth bass both posses spines similar to those of walleye. Mauck and Coble (1971) state that neither of these two species show a particular avoidance of northern pike. The proclivity of walleye to present the dorsal spines toward the predator, seems functionally similar to the habit of *Gasterosteus* tilting its ventral surface, bearing large pelvic spines, towards a perch (Hoogland *et al*., 1956). An attempt at capture of the prey broadside, in either case, would result in a direct strike by the predator on a heavily spined region. In addition, the continuous circling of the walleye prevents the northern pike from preparing for a predatory lunge. In all cases these tactics, of the prey, caused a hesitation by northern pike, which was similar to that described by Hoogland _et al_. (1956). No predatory attempts were made by northern pike during interactions with walleye, which indicates that all study fish had been conditioned by previous interactions. There remains the contingency that, for at least some of the northern pike, the walleye provided were near the maximum acceptable prey size. If this were the case it was a result of the armament of the walleye, since the northern pike did consume other species of prey fish which were larger in body size than the walleye provided.

These findings seemingly contradict earlier statements regarding the high natural level of predation on walleye by northern pike. However, two related facts can explain this apparent conflict. First, data indicate that walleye are most important in the diets of the two largest size classes of northern pike. Second, analysis of prey body depth to predator jaw width ratios indicate that the mean ratio for walleye consumed is slightly lower than that for all species of prey fish combined. Thus the largest predators are consuming relatively smaller walleye as prey. From this it is possible to propose a thesis explaining the high natural use of walleye by northern pike. If the defensive behavior observed were inappropriately employed by these walleye, in the presence of slightly larger northern pike, the result may be an increased ease of capture for the predator. Thus a large northern pike displaying some perseverance might utilize this mistake to its advantage. Hoogland et al. (1956) do indicate that starved northern pike will learn to eat Gasterosteus, even though the predator initially requires extended periods of time to complete the act.

Cannibalism

Of all prey species examined, juvenile northern pike possess the widest range of behaviors and habits which protect them from predation by adult northern pike.

Juvenile northern pike have the ability to detect stationary and partially hidden adults. Other prey species are never noted to display this degree of predator detection ability, but whether this is a result of poorer vision or lower responsiveness than juvenile northern pike is not certain. A juvenile northern pike in open water unerringly avoids any adult it detects. In contrast, other prey fish, such as spottail shiners and white suckers, are occasionally observed to loiter in the immediate vicinity of adult northern pike.

Juvenile northern pike also employ two different methods of escape behavior, with the specific tactic used being contingent upon the nature of the predatory situation. The first type of escape response is used when an adult is detected, at a distance of approximately 0.5 m or more away, orienting or moving towards a juvenile. The escape behavior comprises flight by a series of surface leaps, followed by an underwater dart on an angle, terminated with an abrupt stop. The total effect produced is a series of highly visible stimuli, which attract an observer's attention, often causing the final underwater dart to be overlooked. The tendency, at least for a terrestrial observer, is to project a line along the original path of travel, and extend it beyond the last splash point. This results in a visual search of an area not entered by the prey. The escape behavior combines the traits of both single erratic and multiple lure protean displays (Humphries and Driver, 1970). The surface splashes provide the lure component, while the angular dart and abrupt stop provide the erratic component. Hemmings (1966) gives an account of a similar effect produced by silver colored fishes as they repeatedly change their orientation in the water; this behavior produces a confusing array of erratic flashes of reflected sunlight. The effectiveness of this escape behavior, of juvenile northern pike, is evidenced by the aptness of adults to terminate a predatory attempt with the occurrence of the behavior.

The second escape response occurs when juvenile northern pike detect the presence of an adult observing them within a distance of 0.5 m. Unlike any other prey fish, the juvenile northern pike does not flee, but turns slowly to face the adult. Presumably this allows the juvenile to detect any predatory intention movements of the adult. The turn is mediated by the fins only, with the body held straight. The speed of turning seems sufficiently low to prevent the release of an immediate predatory response by the adult. The slow backing away component of the act does not stimulate the predator to action either. Humphries and Driver (1970) note that fusiform fish are most difficult to see when viewed along the antero-posterior axis. This could suggest that the orientation of the juvenile sufficiently alters the perception of it by the adult to allow the slow backing up to occur. Once the juvenile has reached aquatic vegetation the sudden dart occurs. Vegetation would likely break up the image of the fleeing prey, and so make its progress difficult to follow.

These two escape behaviors, coupled with avoidance of adults by juveniles, could be the basic reasons for the low levels of cannibalism existing in most populations of northern pike.

5. Social Facilitation in Predation

Northern pike were found to be stimulated to activity by observing conspecifics engaged in predatory acts. The behavior pattern displayed by the second individual involves accelerated swimming in the same general area as the perpetrator of the act. Similarity in the behaviors of the two individuals indicates the operation of a type of social facilitation. Hinde (1966) describes social facilitation as, "the performance of a pattern of behavior, already in an individual's repertoire, as a consequence of the performance of the same behavior by other individuals." Social facilitation during feeding activity has been documented for sunfish (Allee, 1951), sharks (Springer, 1967), guppies (Tatsumi, 1972), and numerous other vertebrates. Visual stimuli alone are sufficient to elicit this behavior in northern pike. Frost and Kipling (1967) report a case of attempted food robbing between northern pike fry, presumably stimulated by visual detection of the original predatory act. During the present study two incidents of a similar nature occurred between 10 cm northern pike held in aquaria. Tatsumi (1972) proposes two causes for social facilitation during feeding. Firstly, the "presence recognition effect", resulting from the recognition of the existence of a companion. Secondly, the "feeding recognition effect", resulting from the recognition of feeding behavior by a companion. Northern pike react significantly more often to conspecifics engaged in predatory activities, than to individuals engaged in nonfeeding activities ($p<0.001$). Thus it appears that a stimulus pattern similar to the "feeding behavior recognition effect" (Tatsumi, 1972) elicits the response in northern pike.

In natural situations such feeding facilitation may enhance the utilization of abundant food resources by normally solitary northern pike. The work of Ivanova (1969) documents the occurrence of this phenomenon in the Rybinsk Reservoir. She states that in certain years northern pike form temporary feeding congregations on the spawning grounds of a particularly abundant prey species. She also notes that when prey are more evenly distributed, northern pike are solitary in their feeding habits.

6. Predatory Behavior of Juveniles

The predatory behavior of juvenile northern pike includes most of the salient components of adult predatory behavior. Stalking, appraising, lunging, and pursuing components are shown by juvenile northern pike, albeit in a less refined form. The contention that these behaviors become perfected through experience is also held by Braun (1963). He states that the predatory skill of juvenile northern pike is lower than that of adults. Data show that the predatory success rate realized by juveniles is equal to that of adults. This is made possible by the rudimentary nature of the antipredator behaviors of young prey fish.

Popova (1967) states that "when the young of commercial fish are reared artificially in ponds, they almost never come into contact with predacious fish, and so lack the predator reflex." This may explain, in part, the advantage gained by early spring spawning of northern pike. The young predators are switching from planktivorous to piscivorous habits precisely when the fry of later spawning forage fish are abundant and available.

The predatory act of juveniles does not have the mechanical nature of the adult predatory act. Juvenile northern pike often pause and turn while carrying out predation, where as adults tend to move in straight paths once the act has been initiated. Frost and Kipling (1967) state that young northern pike stalk, flex, and strike at prey, as was similarly observed in the present study. In addition, observations show that juveniles also carry out uninterrupted rushes at nonfleeing prey. The distance from which these rushes occurred (3.0 to 3.5 m) indicate that the detection of prey is likely visual. The tendency of juveniles to continue to rush at stationary prey, without slowing, is in direct contrast to actions of adults in similar situations. Present findings, along with those of Frost and Kipling (1967), show that juveniles will strike at prey from various angles both above and below. This behavior too is in contrast to that of adults, which generally strike at prey on the same plane as themselves.

The general conclusion gained from these brief observations is that to maintain the level of success observed, the ontogeny of predatory behavior of juvenile northern pike must accompany the development of antipredator behaviors by prey species.

C. Social Behavior

RESULTS

During the course of the study 1140 interactions between adult northern pike were observed. In some cases interactions produced no visible alterations of immediate behavior, and thus appeared to be neutral in nature. In other situations aggressive displays or avoidance reactions resulted from interactions which were taken to be of an agonistic nature. An additional portion of the interactions took on the form of positive interactions (ie. when fish tended to remain near one another).

A social interaction, for the purposes of this study, was defined as any encounter between two northern pike in which both participants were aware of one another's presence. In addition, fish were required to be separate from one another for a period of at least five minutes before a second encounter between the same two fish was termed a new interaction.

1. Neutral Interactions

Neutral interactions usually occurred when two fish were moving in opposite directions, and passed parallel to one another. In these situations no positive or negative reaction could be detected in either fish. Neutral interactions were observed to occur in approximately 22% of the interactions in 1973, and in 62% of the interactions in 1974. The observed frequency was significantly higher in 1974 than in 1973 ($p<0.01$, Table 20).

2. Agonistic Interactions

Agonistic interactions between northern pike fell into two general categories. Firstly, interactions in which one of the participants carried out an aggressive display. Secondly, interactions in which one of the participants exhibited an avoidance reaction, even though no display had occurred. In the first case, behavior following the display had a variety of forms depending upon the display situation and the individuals involved. Agonistic interactions arose in 19.5% to 61.0% of the observed interactions (Table 21). The agonistic interactions were composed of approximately 50% display situations and 50% nondisplay situations. Overt aggression, in the form of physical attack, between northern pike was absent during this study. On one occasion the suggestion of attack in the form of pursuit was observed. This situation developed when two northern pike attempted simultaneously to capture the same prey fish, which had been artificially presented.

Northern pike held for observation never developed wounds which could be attributed to intraspecific fighting.

Table 20. Results of interactions between northern pike in 1973 and 1974. Percentages in brackets indicate percent of total interactions in the nondisplay or display section of table. Values in the table indicate the number of times specified fish was observed to give the indicated reaction during interactions.

Abbreviations: F.rem - Fish remains
F.lea - Fish leaves
N.res - Neutral result
M.act - Mutual activity

	No Display		Nondisplay Agonistic			Agonistic Displays				
						case 1		case 2	case 3	
Fish 1973	N.res	M.act	F.lea	F.rem	Total	F.rem	F.lea	N.res	M.act	Total
MP1	9	9	7	16	41	2	5	11	1	19
LF	19	15	10	7	51	0	4	5	1	10
RT	13	11	11	12	47	0	2	2	0	4
JP1	17	2	10	0	29	1	5	1	0	7
JJP1	5	5	5	7	22	0	0	3	0	3
UI	1	4	0	1	6	0	0	0	0	0
*Total 1	64	46	43	43	196	3	16	22	2	43
% of Total 1	(33)	(23)	(44)			(7)	(37)	(51)	(5)	
Total 2	32	23	21.5	21.5	98	3	16	22	2	43

Total interactions 141

*Total 1 - All reactions for all fish.

Total 2 - All interactions between pairs of fish (ie. in interactions with no display occurring two reactions are recorded, one for each participant).

(con't)

Table 20. (con't)

Fish	No Display		Nondisplay Agonistic			Agonistic Displays				
						case 1		case 2	case 3	
1974	N.res	M.act	F.lea	F.rem	Total	F.rem	F.lea	N.res	M.act	Total
E	229	43	25	14	311	7	16	8	1	32
B	113	55	15	12	195	0	1	2	0	3
C	194	34	10	24	262	4	8	5	1	18
D	174	49	19	21	263	1	4	7	0	12
F	195	52	17	18	282	2	8	5	0	15
G	211	43	11	8	273	0	2	2	0	4
X	24	6	0	0	30	0	1	0	0	1
Y	37	8	0	0	45	0	0	0	0	0
W	19	17	0	0	36	0	0	1	0	1
Z	19	17	1	0	37	0	2	5	0	7
I	27	17	0	1	45	1	2	1	0	4
U	12	13	0	0	25	0	0	0	0	0
Total 1	1254	354	98	98	1804	15	44	36	2	97
% of Total 1	(70)	(20)	(10)			(16)	(45)	(37)	(2)	
Total 2	627	177	49	49	902	15	44	36	2	97

Total Interactions 999

Table 21. Comparison of agonistic interactions between northern pike in 1973 and 1974. Percent values in brackets indicate proportion of interactions which resulted in specified behavior.

Year	Number of Nondisplay Agonistic Interactions	Number of Agonistic Display Interactions	Total Number of Agonistic Interactions	Total Number of Interactions
1973	43 (30.5%)	43 (30.5%)	86 (61.0%)	141
	$\overset{\vee}{\vee}$	$\overset{\vee}{\vee}$	$\overset{\vee}{\vee}$	
1974	98 (9.8%)	97 (9.7%)	195 (19.5%)	999

$\overset{\vee}{\vee}$- Indicates significant difference at 1% level.

a. Description of agonistic displays

References to agonistic displays of northern pike have been made previously in the literature, the most notable being those of Svardson (1948), Fabricius and Gustafson (1958), and Frost and Kipling (1967). However, as in most works on the behavior of this species, the first two studies deal with reproductive behavior; the third study deals with the behavior of northern pike fry in aquaria. Postspawning, adult northern pike did display a repertoire of agonistic displays, which were examined during this study. Displays, having the same form as those used during agonistic interactions, occurred in the absence of conspecifics, and possibly functioned as displacement activities. Where applicable these cases will be included in the present discussion.

Branchiostegal display

Branchiostegal display was the type most frequently employed by northern pike during agonistic interactions. Fabricius and Gustafson (1958) report its occurrence between adult male northern pike encountering one another on the spawning grounds.

A branchiostegal display involved opening of the mouth, lateral flaring of the gill covers, and a downward expansion of the gular region. The opercula were involved together with the branchiostegal rays, which were flexed downward and outward, thus stretching the branchiostegal membranes. The display occurred as a single event, or in a sequence of two or three displays (very rarely four). In single displays the mouth was opened and the gill covers were flared to approximately 25% to 30% of the maximum, and the gular region was only slightly expanded. When a sequence was given, the initial display was similar to a single one. The second display was of moderate intensity, with all expansion in the head region developing to approximately 50% of the maximum. The third display was of high intensity, with maximum expansion occurring. If a fourth display occurred it was of similar intensity to the third. The normal sequence, involving three units, required eight to ten seconds to complete, with each gape requiring between one second (low intensity) to three seconds (high intensity). A short pause of one to one and a half seconds occurred between each gape in a sequence.

Fabricius and Gustafson (1958) report that slow forward gliding may occur during this display. In the present study northern pike always ceased forward movement with the initiation of a branchiostegal display. At the point of maximal mouth and gill cover opening, fish occasionally moved slightly backwards. This may result from the rapid erection and forward movement of the paired fins, which Fabricius and Gustafson (1958)[1] observed only during high intensity display. The fin erection and back arching reported by these workers were not observed in the present study, possibly because of the position of the observer in relation to the fish. In most cases it appeared that the paired fins acted only in stablization during the display. It is also possible that flaring of the opercula could have produced a forward-directed force causing the backward movement of the displayer.

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[1] Used slow motion photography to examine behaviors.

In approximately 80% of the displays observed, the displaying fish was positioned in front or slightly to the side of the recipient. The displayer usually faced away from the recipient on an angle. This orientation allowed the exposed gills to be fully viewed by the recipient. The gills appeared as highly visible, bright red areas on a background of white, provided by the light inner surfaces of the gill covers. In some cases the displaying fish was situated behind the recipient, but a portion of these displays may have been visible to the other fish due to the wide visual field of northern pike.

During the study 157 branchiostegal displays were observed (Table 22), of which 110 (70%) were given during agonistic interactions. The remaining 47 (30%) were given in the absence of any conspecifics. The major portion, 41 of these 47, were displays which occurred with no apparent external stimuli evident. These were similar in form to those

Table 22. Summary of all displays observed in 1973 and 1974. Gulping is included as a display type, but is not included in agonistic display totals. Column headings indicate situation in which display took place. Values represent number of times each display occurred in particular situation indicated. Abbreviations used: In = interaction, So = solitary, Pr = predation, Agon = agonistic, BRD = branchiostegal display.

Year and Category	Display Types																		Total Displays	Total 'Agon Displays
	BRD			Snap			Body Waq			Head Shake			Belly Flash			Gulp				
	In	So	Pr	In	So	Pr	In	So	Pr	In	So	Pr	In	So	Pr	In	So	Pr		
1973																				
Totals	36	14	3	3	3	1	4	5	0	0	0	0	0	0	0	1	2	0	72	43
% Total Displays		73			10			13			0			0			4			
% Agon Displays		84			7			9			0			0			-			
1974																				
Totals	74	27	3	9	16	7	4	8	1	4	1	0	6	2	0	2	4	1	169	97
% Total Displays		61			19			8			3			5			4			
% Agon Displays		76			10			4			4			6			-			
1973-74	110	41	6	12	19	8	8	13	1	4	1	0	6	2	0	3	6	1	241	140
Total		157			39			22			5			8			10			
% Total Displays		65			16			10			2			3			4			
% Agon Displays		79			9			5			3			4			-			

displays given during interactions. The remaining 6 of the 47 occurred following unsuccessful predatory attempts.

Snapping display

Snapping display, as well as all other displays, had a much lower frequency of occurrence than branchiostegal display during agonistic interactions. Snapping display is not mentioned in the literature, except for the reports of rare cases of nipping between males while spawning (McNamara, 1937; Fabricius and Gustafson, 1958). The snapping display, unlike nipping was never directed toward the opponent, but occurred with the displayer parallel or perpendicular to the second fish.

This display consisted of a series of very rapid, minor mouth openings and closings; a series contained between 10 and 20 repetitions. The length of a series was variable, with a display rate of approximately 4 or 5 snaps per second. The distance the mouth was opened - approximately 25% of the maximum gape - remained constant throughout the display sequence. The gill covers did not appear to be flared during this display. Prior to the display the northern pike was usually stationary or cruising slowly. With the inception of snapping the displayer accelerated rapidly, in open water, approaching burst speed. With termination of snapping the locomotory movements also ceased, and the displayer glided passively to a halt. When this display was performed during an intraspecific interaction, the direction of travel of the displayer was either away from or across in front of the recipient. The path of travel was observed to be along an arc in most cases, which may be attributed to the confining effects of the observation area. The most visible portion of the display was the rapid snapping of the mouth, particularly when the fish was traveling across in front of the viewer.

During the study, 39 separate snapping display sequences were observed (Table 22), of these 12 (31%) were given during agonistic interactions. The largest portion, 19 (49%), occurred in the absence of other northern pike, with no external stimuli apparent. The remaining 8 (20%) occurred following unsuccessful predatory attempts.

Body wag display

The body wag display was observed infrequently during interactions between northern pike. Svardson (1948) refers to a "synchronous swimming standstill" occurring between males and females during the spawning act of northern pike. This may be somewhat similar in general form to the body wag display observed during the present study.

This display consisted of a series of exaggerated carangiform swimming movements carried out by a stationary fish.

During these movements the displayer held the anterior portion of its body several centimeters lower than the posterior. As swimming movements were initiated, the pectoral fins were ventrolaterally projected and rotated to the vertical plane, and then began to beat weakly forward. The swimming motions of the trunk were accentuated by their abnormally high amplitude and low frequency. Very little lateral head movement resulted, suggesting that a minimum of propulsive force was generated by the body undulations. A body wag display consisted of from two to four complete swimming cycles (a cycle being movement of the tail across the midline to one side and then returning across the midline to the starting position). Each cycle required approximately two to three seconds to complete. In most cases the recipient was located lateral to and slightly deeper than the displayer. Following termination of the body wag, the displayer usually moved slowly away from the area of interaction, using normal locomotory movements.

Of the 22 body wag displays observed, only eight (36%) occurred during agonistic interactions. The major portion, 13 (59%), were given by solitary northern pike in the absence of any apparent external stimuli. The display was observed only once following an unsuccessful predatory attempt.

Belly flash display

This display occurred very seldom, and was employed by only two fish during the study. No references to this type of display are given in the works on spawning or fry behavior of northern pike.

This display was only performed in open water areas. When used during agonistic interactions it was conducted in front of or lateral to the recipient. The displaying fish, which was stationary or moving slowly, initiated the sequence near the water surface. Acceleration to moderate swimming speed occurred parallel to the surface. The displayer then veered sharply downward on an angle of approximately 45°, and accelerated to near burst speed. The path of travel became parallel to the substratum approximately 0.05 to 0.10 m from it. At this point the fish rolled to its side. Forward movement continued as the ventral surface was briefly presented toward the recipient. The presentation occurred one or two times during a single display, with each presentation lasting approximately 0.50 to 0.75 seconds. After the last presentation the displayer veered upward, and slowed as it approached the surface. On two occasions several minor mouth snaps occurred subsequent to the belly flash display. The most striking feature of this display was the brief flash of white from the light underside of the fish.

Belly flash displays were observed eight times during the study, with six of these displays occurring in the presence of conspecifics. The remaining two displays were given by solitary fish, and no displays were observed in relation to frustrated predatory attempts.

Head shake display

Head shaking was the least frequently observed agonistic display used by northern pike. Fabricius and Gustafson (1958) report "repulsive head shaking" by unripe female northern pike when approached by courting males on the spawning grounds.

As in most other agonistic displays, the head shake occurred beside or in front of the recipient fish. The displayer usually held its body parallel or perpendicular to the opponent's head. The displaying fish then swung the anterior third of its body violently from side to side. The head was moved in a complete arc from one side to the other, and did not stop at the midline as it did during prey turning movements. Display duration was approximately two to three seconds, with the head completing five to ten arcs in this time.

Of the five head shake displays observed, four were conducted during agonistic interactions. The remaining one was given by a solitary fish.

Gulping

Another activity carried on by northern pike was surface gulping. It was unclear whether or not this maneuver functioned as an agonistic display. It did occur at very low levels during intraspecific interactions, but appeared to lack any specific recipient-orientation component. Hence, it was not included as an agonistic display, but will be described for the purpose of documentation.

At the onset of a gulping act the northern pike was always deep in the water column. The fish swam slowly forward, rising gradually to the surface. As the surface was reached the jaws of the fish were opened partially and pushed above the surface. The head described a small arc out of the water, and returned with an audible plop. The fish then continued forward for 0.5 to 1.5 m parallel to the water surface. Next, the fish angled downward in a shallow dive, and swam slowly toward the bottom. At a variable distance from the surface (usually about half way to the bottom) a stream of air bubbles escaped from the gill chamber on either side of the head. The fish usually continued swimming slowly forward near the substratum following this act.

Gulping acts were observed 10 times during the study, with three (30%) occurring within sight of conspecifics. In all of these cases the displaying fish showed no intrest in the second individual. Of the remaining acts, six (60%) were given by solitary fish, and a single act was observed to occur following an unsuccessful predatory attempt.

b. Nondisplay agonistic interactions

The second type of agonistic interactions were those in which two fish showed differing tendencies to remain in the area of encounter. This situation arose when two fish met one another, the result being the departure of one fish while the other remained. In no case was any form of threat behavior observed to occur. The individual moving away usually traveled slowly, and flight from the area was never observed. It appeared that these situations represented low level agonistic interactions, and may have performed a function in spacing of individuals.

c. Quantitative analysis of agonistic behavior

1973 and 1974 levels

From Table 21 it is apparent that the levels of aggression, as indicated by the frequencies with which interactions took on an agonistic nature, were much higher in 1973 than in 1974. The frequencies of all types of interactions combined in 1973 were much lower than in 1974, with 0.96 and 1.68 interactions per hour per fish occurring respectively. However, the percentage of interactions resulting in agonistic behavior was significantly higher in 1973 (61%) than in

1974 (19.5%) ($p<0.01$). Agonistic displays and avoidance reactions, examined separately, were both significantly higher in the first year ($p<0.01$). This paradox appears to be related to the levels of activity and predation extant in the two study fish populations. This situation will be examined separately.

Male and female aggression

During this study no general, basic differences in the behavior of male and female northern pike were evident. Levels of agonistic displaying were used as an indication of the aggressiveness of each sex. In both years the percent of interactions resulting in agonistic display was very similar for males and females (Table 23). In neither year was the difference significant.

Nondisplay agonistic interactions were also examined in relation to the sex of the fish involved. In this situation neither fish appears to indicate overt aggressiveness to the other by any specific act. However, it is possible that one sex may tend to show greater avoidance than the other. In 1973 neither sex showed a greater tendency to leave during nondisplay agonistic interactions ($p>0.05$, Table 24). In 1974 males tended to leave the area with significantly greater frequency than females ($p<0.05$). This difference may relate to some general dissimilarity between the sexes in 1974.

Table 23. Comparison of female and male northern pike display rates in 1973 and 1974. Values indicate number of times particular situation was observed. Differences tested for significance at the 5% level by Chi-square for independence.

Year	Female Displays	Female Interactions		Male Displays	Male Interactions
1973	26	136		17	103
	(% Display = 19.1)		≯	(% Display = 16.5)	
1974	31	511		66	1390
	(% Display = 6.1)		≯	(% Display = 4.7)	

≯ - Indicates no significant difference at 5% level

Table 24. Comparison of tendencies of female and male northern pike to leave the area following interactions without displays. Differences tested for significance by Chi-square for independence.

Year	Females Leave	Female Interactions		Males Leave	Male Interactions
1973	23	110		20	86
	(% Leave = 20.9)		≮	(% Leave = 23.3)	
1974	11	480		87	1324
	(% Leave = 2.9)		<<	(% Leave = 6.5)	

<< - Indicates significant difference at 1% level.

Fish size and aggression

The relative sizes of northern pike involved in interactions were examined. This was done to determine if the size of an individual dictated the levels of aggression it would show during interactions with larger and smaller fish. The fish studied were ranked according to a size value obtained from the formula - Length x Weight/10,000. This provided an estimate of the bulk of an individual rather than just a length or weight value.

The levels of agonistic displaying carried on by all fish were analysed according to the relative sizes of the displayers and recipients (Table 25). In 1973 the average display frequencies, of the smaller and larger fish involved in interactions, were 19.4% and 24.5% respectively (Table 25). The difference between these display levels was not significant ($p>0.05$). Similarly, in 1974 the display rates of smaller and larger fish, 4.8% and 6.0% respectively, were not significantly different.

The tendency of the displayer to leave the area of interaction was also examined in relation to the relative sizes of displayer and recipient. In both years there was no significant difference ($p>0.20$) between the tendencies of larger and smaller displayers to leave the area (Table 26).

Table 25. Summary of the number of agonistic displays given by northern pike to opponents which were larger or smaller in relative size. Relative size obtained from the formula - Length x Weight / 10,000. Significance of differences tested by Chi-square for independence. Abbreviations use: Inter = interaction, Disd = displayed to.

	Relative Size of Opponent							
	1973				1974			
	Larger		Smaller		Larger		Smaller	
	Disd	Not Disd	Disd	Not Disd	Disd	Not Disd	Disd	Not Disd
Outcome of Inter	19	98	24	98	43	902	54	902
Percent	16%	≮	20%		5%	≮	6%	

≮ - Indicates no significant difference at 5% level.

In nondisplay agonistic situations, since aggression did not appear to be communicated by a ritualized act, it may be expected that some external characteristic would determine whether or not a fish was avoided by a conspecific. Using the same size ranking classification, the nondisplay agonistic interactions were examined (Table 27). In 1973 the smaller fish involved in this type of interaction tended to show avoidance in 70% of the cases, which was significantly greater than that shown by the larger fish ($p<0.01$, Table 27). In 1974 the situation was similar, with the smaller fish leaving in 59% of the interactions of this sort. This difference was also significant ($p<0.05$, Table 27). The effect of size on the nondisplay agonistic interactions may help to explain the differences which appeared between males and females in 1974 during these interactions. In 1974 a wider range of fish sizes were used, with females tending to be larger relative to males than in 1973. Thus the smaller relative size of males in 1974 may account for their higher tendency to leave the area of interaction.

Consistency of agonistic displays

Although aggression, as measured by the frequency of agonistic displays, was higher in 1973, the types of displays employed were very similar in both years. In relation to the total displays given in each year, the levels of branchiostegal, snapping, and body wag displays used were similar

Table 26. Summary of agonistic display interactions between northern pike, and the tendancy of the displayer to leave when opponent is larger or smaller in relative size. Chi-squared for independence applied. Abbreviations used: St = stays, Le = leaves. Values indicate number of times the specific behavior was observed to occur.

	Relative Size of Opponent							
	1973				1974			
	Larger		Smaller		Larger		Smaller	
	St	Le	St	Le	St	Le	St	Le
Behavior of Displayer	1	11	2	5	5	22	10	22
Percent		92%	≯	71%		81%	≯	69%

≯ - Indicates no significant difference at 5% level.

Table 27. Summary of nondisplay agonistic interactions, and the tendency of a northern pike to leave the area when opponent is larger or smaller in relative size. Chi-square test for independence applied. Abbreviations: same as in Table 26. Values indicate number of times specified reaction occurred.

	Relative Size of Opponent							
	1973				1974			
	Larger		Smaller		Larger		Smaller	
	St	Le	St	Le	St	Le	St	Le
Behavior of First Fish	13	30	30	13	40	58	58	40
Percent		70%	>>	30%		59%	>	41%

>> - Indicates significant difference at 1% level.

> - Indicates significant difference at 5% level.

in 1973 and 1974 (Table 22). The two new displays employed in 1974, head shake and belly flash, occurred at such low levels that it was statistically possible that neither would have been seen in 1973. The various types of displays did not appear to require different types of stimuli to trigger their occurrence. The different types of displays did not appear to represent different levels of threat. This was suggested, since in a year when agonistic displays occurred more frequently (1973), the proportions of the various displays employed did not differ significantly from the proportions observed in a year with lower levels of agonistic behavior (1974). It is possible that subtle differences existed between the attitudes and intensities of the displays given in each year, and that these were not detected. Refinement of observation techniques (ie. slow motion photography) may be required to elucidate differences between displays which superficially appear similar.

Effects of agonistic displays

The five agonistic displays employed by northern pike did not appear to differ in their effects on the outcome of aggressive interactions. The post-display behavior of both displayer and recipient was variable, thus reducing predictability of the outcome. Due to this variability a clear pattern of dominant-subordinate relationships was not apparent for this species. Recipients of agonistic displays were never observed to flee from the area of interaction, nor did they assume any obvious appeasement postures suggestive of subordinance. The most extreme result of agonistic displays was slow movement by one of the participants away from the area of interaction.

The outcomes of agonistic display interactions could be grouped into three main categories. Firstly, cases in which one of the participants showed a higher tendency to leave the area of interaction. This category could be further subdivided as to which fish remained and which fish left. Secondly, cases in which neither fish showed a differential in the tendency to leave or remain. This category contained the cases in which both fish left the area, plus those cases in which both fish remained in the area. Thirdly, those rare cases in which the participants performed some mutual or positive social activity together following a display.

There was a high degree of similarity between 1973 and 1974 in most of the possible outcomes of agonistic display situations. In 1973, the displayer left the area of interaction in 37% of the cases, while the recipient left in 7% (Table 20). In 1974, the displayer left in 45% of the interactions, and recipients left in 16%. In both years the displaying fish tended to leave significantly more often than the recipient ($p<0.01$). Comparing each of the four categories, under agonistic displays (Table 20), between

1973 and 1974 indicates that there was no significant difference between the levels in any single case (p>0.15).

3. Positive Interactions

Northern pike did enter into very simple positive interactions with one another, and these appeared to have a mutually beneficial value. The interactions did not occur solely by chance, since on several occasions individuals attempted to facilitate interactions by following conspecifics. Parallel swimming was the usual activity adopted during these interactions. On occasions parallel swimming terminated with the participants remaining near one another for extended periods. During these interactions individuals physically contacted each other frequently. Contact occurred along the sides of the fish while they were swimming or stationary. Another form of contact involved one participant placing its lower jaw region on the dorsal surface of the other fish. No aggressive responses ever developed during these positive interactions. The levels of positive interaction were low and virtually identical in both years of the study (Table 20).

4. Social Structure

Although northern pike tended to be solitary in their habits, they did interact with one another in the manners described. The absence of attack and the use of ritualized displays during intraspecific interactions suggested the existence of a social framework.

Dominance relationships

Agonistic interactions, in some cases, suggested that superficial dominant-subordinate relationships existed between certain northern pike observed. These relationships did not fall into a clear hierarchical pattern, since individuals would assume the role of dominant, subordinate, or equal in a series of interactions with one other northern pike. Only in a very few cases could a consistent pattern of social relationships between two individuals be discerned.

The size of fish did not effect their tendency to give agonistic displays, or their tendency to leave after displaying. As stated, size was a factor in nondisplay agonistic interactions, where larger individuals were avoided most frequently. Sex-related dominance characteristics appeared to be a result of size differences only, and therefore were not actually sex-related.

Examination of relationships between specific individuals did suggest that a type of dominant-subordinate association could develop between northern pike in confinement.

The relationship which developed between fish MP1 and fish JP1 during observations in 1973 represented the most stable social relationship observed. JP1 was the smaller fish, and tended to avoid interactions with most other northern pike. The relationship between these two fish became apparent when MP1 was removed from the observation area, and JP1 was seen to increase its activity. The positions of these fish at the beginning and end of the observation periods were used to determine the areas used most frequently. MP1 ranged widely over the lower half of the observation channel (Figure 20). This fish was removed between the 26 and 27 observation periods. JP1 was present from the 8 to the 26 observation period together with MP1 (Figure 21). During this time JP1 spent much time within the general range of MP1. However, JP1 avoided interactions with other fish by remaining inactive for extended periods in the weed bed on the bottom of the lower pool (Table 28). Following the removal of MP1, the habits of JP1 changed, so that this fish was observed outside the weed bed 40% more often (Figure 22 and Table 28). This type of situation might not have developed to such an extent in free-ranging northern pike. However, the upper half of the observation area was used to a lesser extent than the lower half, yet JP1 never showed a tendency to restrict its activities to that area.

Table 28. The location of fish JP1 in the observation area at the begining and end of observation periods, with fish MP1 present and absent. Values indic- number of times JP1 observed in specified area.

Observation Periods 1973	Location of JP1	
	In pool bottom vegetation	Outside pool bottom vegetation
8 to 26 MP1 present	8 (50%)	8 (50%)
	∨	∧
27 to 33 MP1 absent	1 (10%)	9 (90%)

∨- Indicates significant difference at the 10% level.

Table 29. Summary of temporary site attachments developed by northern pike in the observation area. To qualify the site attachment must be at least three days in duration. Size of area given in square meters.

Fish	Area Coordinates*	Size of Area	Dates of Occupation	Days Duration
1973				
JP1	K to O:37 to 42	2.3	July 7 - Aug 7	31
JJP1	J to P:13 to 17	3.3	Aug 23 - Aug 28	5
RT	A to D:42 to 52	2.3	July 5 - July 14	10
1974				
C	N to P:24 to 28	1.4	June 6 - June 19	14
D	B to D:42 to 51	2.3	June 25 - June 27	3
B	A to C:43 to 50	1.6	June 27 - July 3	7
B	A to C:42 to 50	1.8	July 10 - July 13	3
W	A to C:42 to 51	2.0	July 31 - Aug 5	6
F	N to R:35 to 39	2.3	June 15 - June 20	5
G	H to M:36 to 39	2.2	May 28 - May 30	3

* - Refer to APPENDIX 2.

It appeared that the avoidance tendencies were strong enough to cause a restriction of activity, but not strong enough to cause emigration of JPl. For other northern pike the relationship between individuals was not this clear, and mutual tolerance tended to prevail in most cases.

Spatial relationships

The observed system of space allocation employed by northern pike did not fit easily into the classical scheme of territories or home ranges.

Northern pike were observed to spend a major portion of the daylight hours isolated from one another. This was a result of several general habits of this species. Firstly, the fish remained inactive for extended periods in areas of cover or aquatic vegetation, thus effectively cutting off visual contact. Secondly, interactions with conspecifics were sometimes avoided. Thirdly, agonistic displays were used in aggressive manners, which frequently terminated interactions. However, this solitary nature was variable and by no means absolute. As mentioned, northern pike were observed to interact with one another in positive manners, and at times appeared to exhibit appetence for these interactions.

Northern pike did not hold territories (in the classical sense); they usually ranged over the area showing no particular preference for a single territory. Individuals did develop what might be better termed temporary site attachments. These sites were specific areas which individuals tended to use repeatedly over a variable number of consecutive days. During periods of temporary site attachment fish also used other segments of the available habitat, but they tended to return more frequently to the temporary site than to any other area. The variability between individuals was large in this respect. The site attachments lasted from several days or weeks in the case of fish C (Figure 23), to a month in the case of fish JP1 (Figure 21). Site attachment could cease abruptly, for no apparent reason. Fish might then develop a new temporary site, or revert to general nonpatterned use of the whole area. In contrast, certain individuals always displayed general use of a large area, as did fish MP1 (Figure 20).

Certain features were characteristic of temporary site attachment. Firstly, sites were usually centered around structural irregularities in the environment. Logs protruding into the water, openings in aquatic vegetation beds, particular vegetation beds, bank indentations, and specific over-hanging riparian vegetation all seemed to serve as environmental reference points. Secondly, most temporary sites were associated with cover, so that residents were not in open view. Thirdly, fish were repeatedly observed to remain inactive for extended periods in these areas. Fourthly, the site was not actively defended by the resident fish, and intruders were usually tolerated. However, intrusions by conspecifics occurred seldom in most cases. Agonistic displaying by residents of temporary sites did not center around the site. Fifthly, obvious contests for temporary sites never occurred. Sixthly, sites were not situated in relation to one another so as to apportion the available space into equal sized parcels.

The cases of fish C and D from 1974 illustrate two levels of site attachment observed during the study. Fish C displayed the most obvious and consistent case of temporary site attachment in 1974. From June 6 to 19 this individual showed a distinct preference for a vegetated area on the north side of the main channel of the observation area (Figure 23). All of the observations, except one, of this fish within the 30% isopleth in Figure 23 were recorded between June 6 and 19. This site was associated with four small posts driven into the substrate in the form of a square, with the posts 0.3 m appart on a side. During daily observations, fish C was repeatedly observed to return to this spot, and pass through or remain inactive there for a period of time. On four occasions fish C and fish F met in area of C's temporary site. In one case F left slowly while C remained, and in the other three cases both fish left the area. In no case was aggression displayed by either fish. After June 19, C stopped using this site, and was noted in that particular area only once thereafter.

Fish D was frequently noted active and inactive in the area of the lower screen between June 25 to 27 (Figure 24). The area used by D was larger than that used by C, and the period of use was much shorter. Unlike C, D did not use a specific small site for periods of inactivity, but rather used the general region near the lower screen.

Including the two fish mentioned, seven cases of temporary site attachment were observed in 1974, and three were observed in 1973 (Table 29). The size of the areas used and duration of use showed some variation between individuals, and also between sites used by one individual. The average size of these sites was approximately 2.1 m^2.

Range

Realizing the inherent limitations of studying home range habits in a confined situation, some information pertaining to this aspect of northern pike behavior can be gleaned from other observations made during the study.

Data obtained suggest that northern pike did restrict the size of the area over which they ranged. As mentioned, fish in both years were observed to be present in the lower

Figure 20 to 24. Maps of areas used by individual northern pike in 1973 and 1974. Dots represent observed position of fish at beginning or end of observation period. Isopleths are approximations of the smallest area within which the fish was observed 30, 50, 70, and 90 percent of the time.

Figure 20. Positions occupied by MP1. Observation periods 1 to 26, 1973.

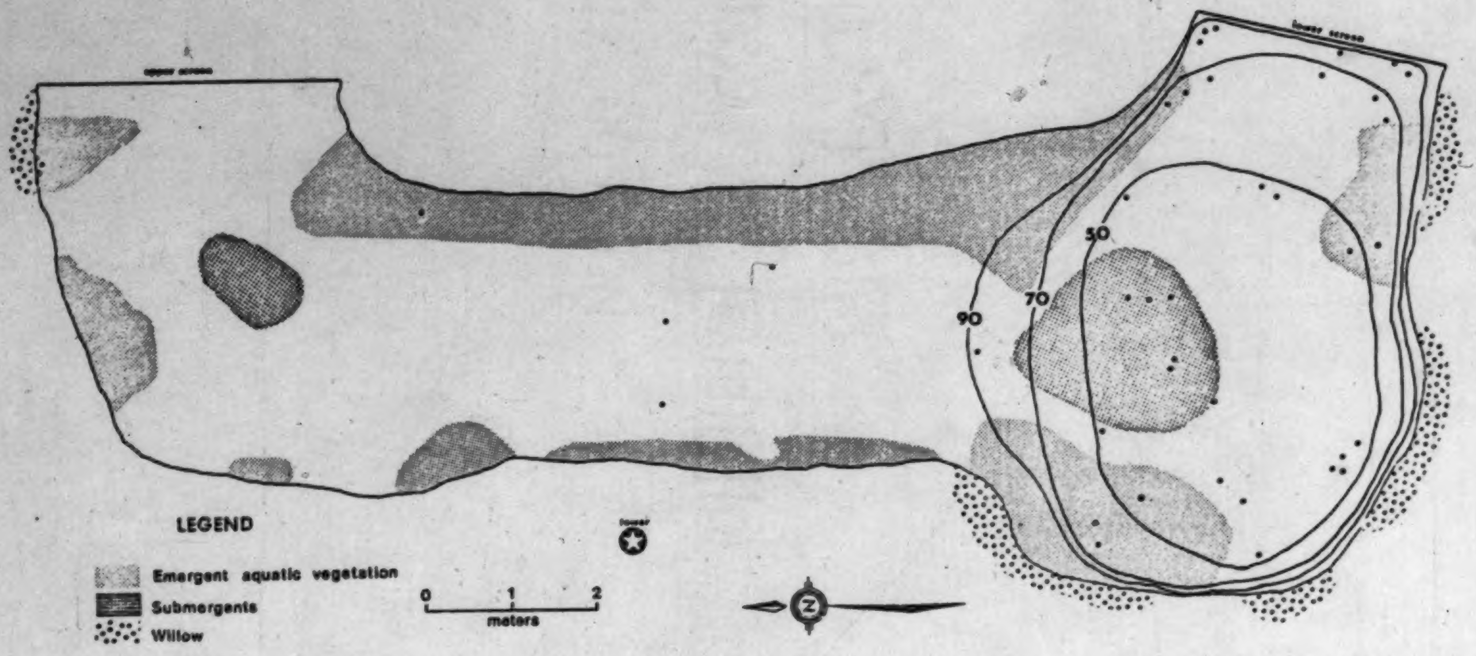

upper screen
lower screen
50
70
90
LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters
N

Figure 21. Positions occupied by JP1. Observation periods 8 to 26, 1973.

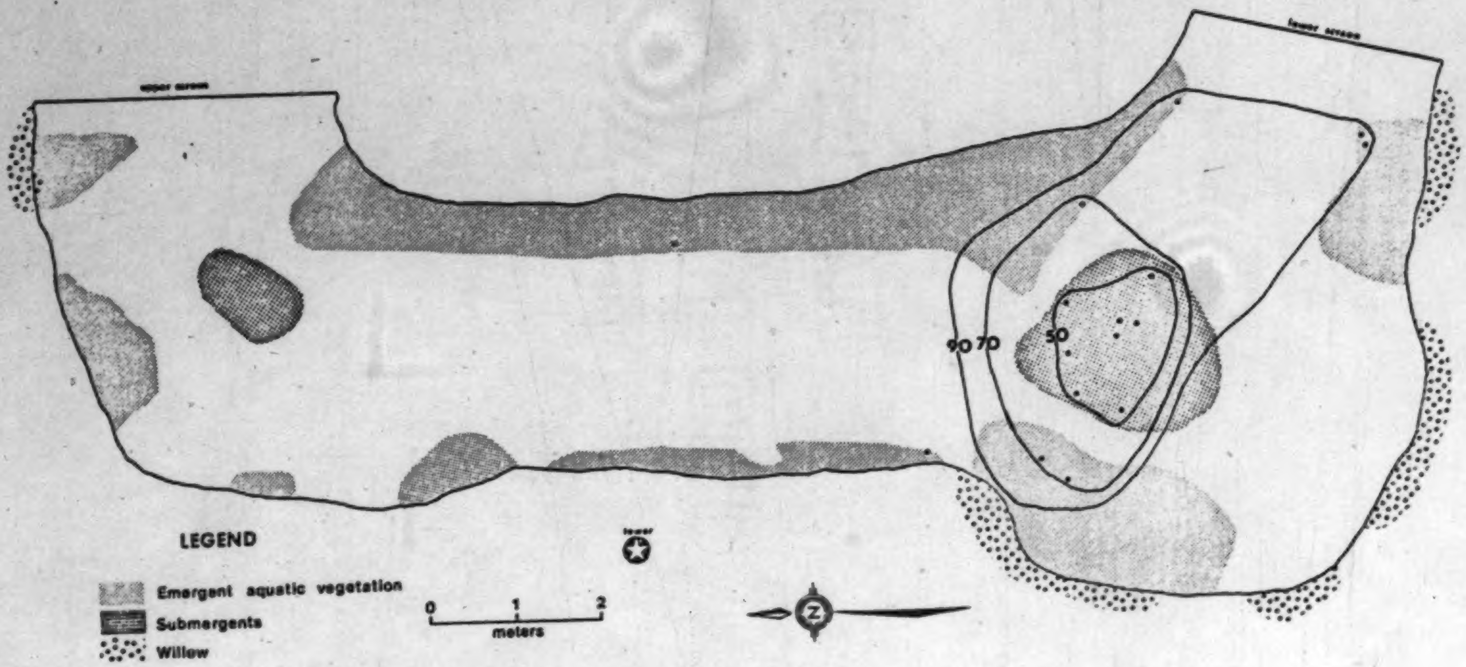

upper stream
lower stream
90
70
50
tower
LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters
N

Figure 22. Positions occupied by JP1. Observation periods 27 to 33, 1973.

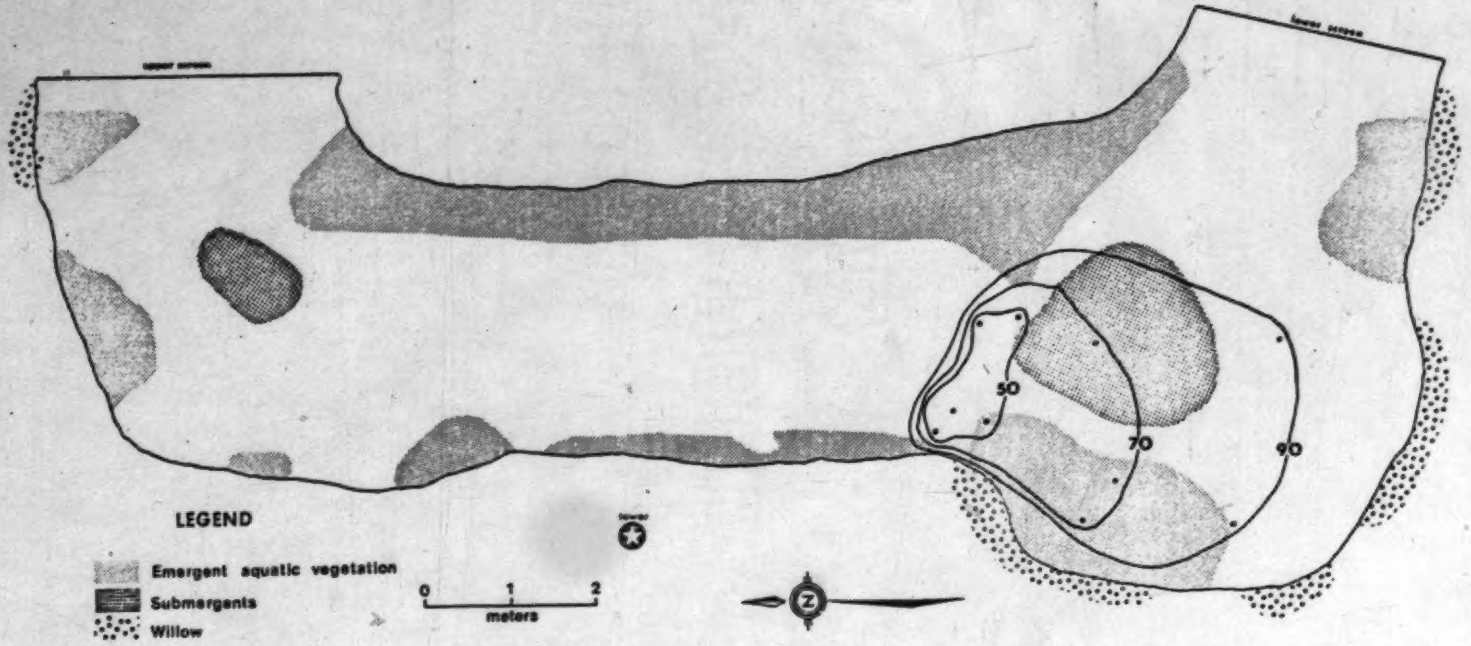
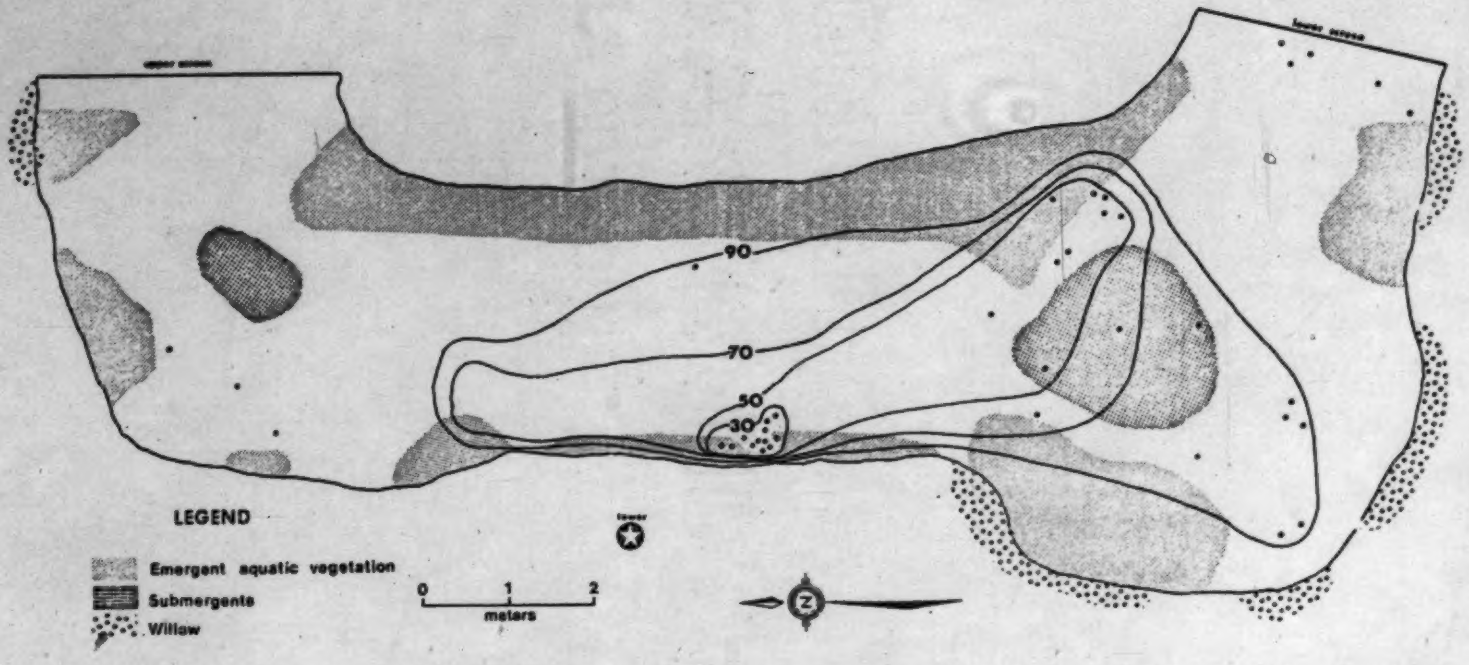
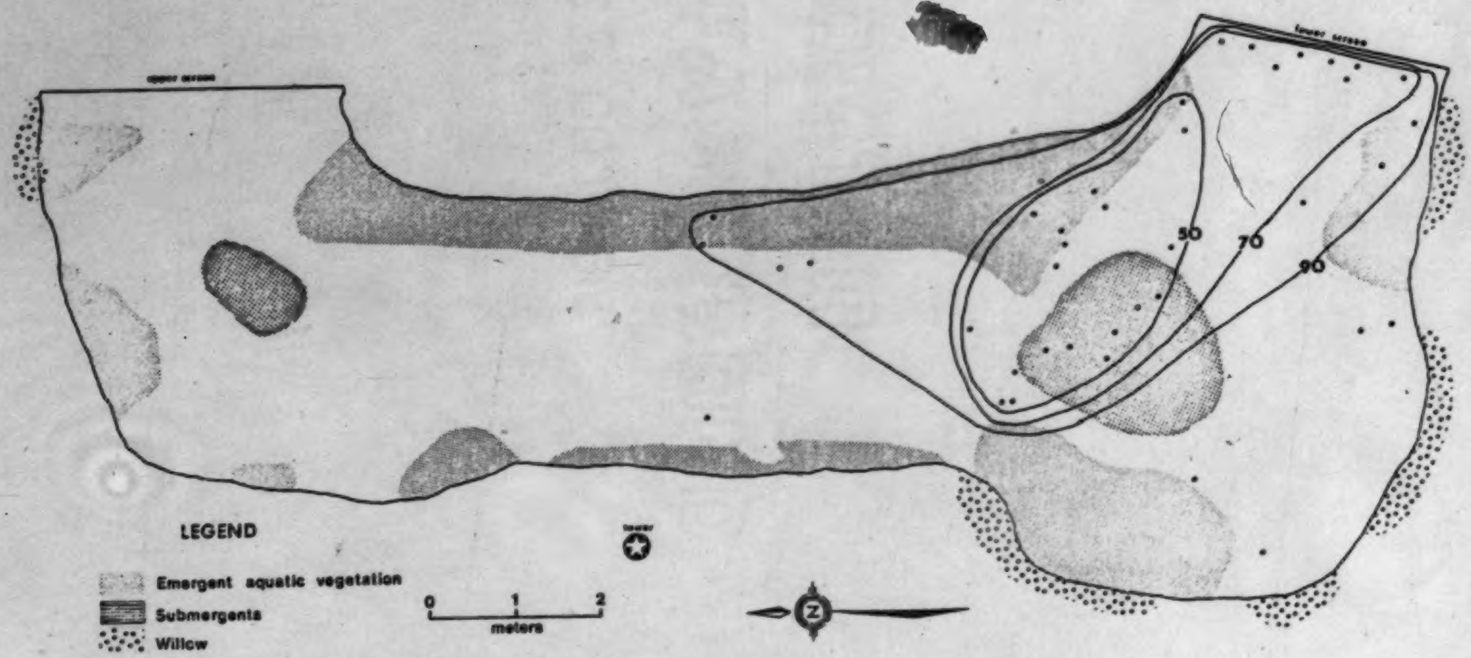

50
70
90
LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters
N

Figure 23. Positions occupied by C. Observation periods 1 to 23, 1974.



lower screen
90
70
50
30
tower
LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters
N

Figure 24. Positions occupied by D. Observation periods 1 to 21, 1974.


lower screen
50
70
90
LEGEND
Emergent aquatic vegetation
Submergents
Willow
0
1
2
meters
Z

half of the observation area more often than in the upper half.(Table 30). The difference between the observed and expected use of the two areas was highly significant ($p<0.01$). What ever the specific reason for the preferential use of the lower area, this does show that northern pike did exhibit range restriction. These data also indicate that densities of fish used in the observation channel were probably not too different from those occurring in the natural environment. Fish were never observed to develop any specific paths of travel through the study area, except for the general tendency to move in areas of cover. Regular patterns of patrolling specific areas were never observed. The general empression gained was that northern pike tended to move randomly throughout a limited area of preferred habitat. A high degree of overlap of ranges did exist, mainly in the lower portion of the observation area (ie. Figure 23 and 24). As a result frequent interactions between individuals occurred. As described previously, the nature of these interactions was highly variable, and bore no relation to the specific area in which they occurred.

Individuals showed day to day variations in the general area of the observation channel frequented. Fish that had temporary site attachments showed less variability of space utilization when close to their site. However, travel by these individuals in areas more than two or three meters away from the site again appeared to have no fixed pattern.

The total size of the area over which an individual traveled also showed day to day fluctuations. This was seemingly due to the level of activity on any particular day. The daily distance traveled by fish in 1973 ranged from a minimum of zero meters per hour to a maximum of 40 m per hour, averaged over the whole day. Individual fish showed differences in mean hourly distances traveled per day over the summer (Table 31), the average being approximately 8 meters per hour for fish in 1973. In a normal 10 hour summer day this would give a northern pike a linear range of nearly 0.1 km, or a circular range with a diameter of from 25 to 30 m. These values could be increased by as much as two times, since fish watched in 1974 were about twice as active as fish watched in 1973.

Table 30. Observed and expected use of upper and lower portions of observation area. Positions of all fish recorded at begining and end of daily observation periods. Expected use calculated from total area of habitat available in each portion of the channel, assuming no preferences existed. Values indicate number of separate observations of fish in specified area. Chi-square for independence applied.

	Position of Fish in Observation Area					
	Upper (35% total area)			Lower (65% total area)		
Year	Observed Use		Expected Use	Observed Use		Expected Use
1973	18		67	173		124
1974	41		122	308		227
Total	59	<<	189	481	>>	351

>> - Indicates significant difference at 1% level.

Table 31. Distances traveled per hour per day by northern pike observed in 1973. Values determined from tracing fish travel paths on scale map.

	Distances Traveled in Meters per Hour by Fish					
Category	MP1	LF	RT	JP1	JJP1	UI
Average	6.3	11.3	9.3	6.1	6.9	6.9
Maximum	18.7	37.1	35.4	39.8	33.4	13.1
Minimum	0.0	0.0	0.0	0.0	0.0	0.0

Mean distance traveled by fish = 7.8 m/hour/day.

DISCUSSION

Northern pike have been described as being solitary in their habits (Wich, 1958; Nursall, 1973). Leyhausen (1965) notes that field research concerned with the social behavior of such species, outside of the breeding season, is rare. In situations where high densities of a solitary species develop, intraspecific interactions are inevitable; it seems imperative that solitary animals too require a social framework to dictate the actions of individuals when interactions occur. For predatory species a system of social behaviors, which ritualize aggressive acts and minimizes detrimental physical conflict, would have distinct functional importance at high population densities (Lorenz, 1952). From field observations it is evident that northern pike are not spaced evenly throughout the available habitat, as would be expected if these fish showed only repulsion for one another. Leyhausen (1965) proposes that some centripetal tendencies must exist in populations of solitary species to cause individuals to retain contact with one another.

Northern pike do interact with one another, albeit at low frequencies. From observations made during the present study, it is apparent that a system of social guidelines is followed during these interactions. This system is apparently functional in reducing detrimental fighting, since physical combat between individuals was absent from study fish populations.

Interactions between adult northern pike can be separated into three general categories encompassing all cases observed. These are neutral interactions, agonistic interactions, and positive interactions. Agonistic behavior, because of its greater frequency and variability, is the major aspect of social behavior considered here.

1. Neutral Interactions

Interactions were considered to be neutral in nature, when individuals passed within four meters or less of each other, but showed no positive or negative reactions. It is possible that visual inspection and appraisal of conspecifics occurred in these cases, but because of the observational system employed this was not detectable. Neutral interactions are not ment to imply social indifference, but merely the failure of either individual to display overt dominant or subordinate tendencies. Collias (1944) suggests that subtle forms of aggressiveness can be shown by simple independence of action, while submissiveness can be shown by avoidance. These forms of behavior seem to exist in neutral interactions of northern pike, as they do in those of free ranging cats (Leyhausen, 1965). Leyhausen (1965) reports that frequently when two cats meet in a neutral area (ie. hunting paths) neither individual displays dominance or subordinance, but each concedes some ground to facilitate unrestricted passage of the conspecific. Presumably, in a situation where a resource is not being directly contested it is advantageous for both individuals to maintain neutrality by displaying a level of tolerance. Morse (1974) notes that the low number of overt aggressive interactions occurring in the wild suggest that mutual avoidance fulfills an important role in niche partitioning.

The nature of a social system is dynamic (Crook, 1970), and the pattern of behavior employed during interactions is sensitive to individual needs (Marler, 1956; Stokes, 1962). In 1974, 62% of the interactions between northern pike were neutral in form, while in 1973 only 22% of the interactions were of this type. These data suggest that in the second year of the study, fish displayed far greater mutual tolerance for one another. Food resources were lower in 1973 than in 1974. Although other factors may also be involved, it appears that a change in the availability of a population resource has affected a corresponding change in social behavior. Errington (1939) notes a decline in mutual tolerance between muskrats under conditions of food shortage. Collias (1944) agrees that hunger is a potent factor helping to determine the degree of intragroup tolerance.

On the basis of present findings it is apparent that mutual tolerance is a basic component of the social strategy of northern pike. However, levels of tolerance may be modified in relation to levels of resource availability. Findings of Ivanova (1969) lend support to this conclusion.

She found that northern pike become more solitary in their habits during times of low food availability.

2. Agonistic Behavior

Interactions between northern pike were classified as agonistic when an aggressive display or avoidance reaction occurred. Agonistic interaction levels appear to be inversely correlated with those of neutral interactions (Table 20). However, the proportions of display and nondisplay agonistic interactions remain approximately equal regardless of the total frequency of agonistic interactions (Table 20 and 21). Zack (1974) reports that in Hermissenda a change in overall proportions of interactions which are agonistic does not alter the pattern of agonistic behaviors employed. Overt physical violence does not appear to be a characteristic of the agonistic behavior of post-spawning northern pike, under natural conditions. This may suggest that levels of aggression are lower during the nonbreeding season, since McNamara (1937) and Fabricius and Gustafson (1958) report observations of males of this species fighting on the spawning grounds.

a. Description of Agonistic Displays

In the present study northern pike employed six types of agonistic displays during intraspecific interactions. Svardson (1948) and Fabricius and Gustafson (1958) note the use of two types of displays by northern pike during

during spawning activities. Several of the displays occur infrequently in the absence of conspecifics; in these instances it seems that the displays fulfill a displacement function.

Branchiostegal display

This display consists of simultaneous mouth opening, opercular flaring, and downward bulging of the gular region. Similar displays occur in Salmo (Kalleberg, 1959; Keenleyside and Yamamoto, 1962), Stichaeus (Farwell and Green, 1973), numerous genera of cichlids (Baerends and Baerends-Van Roon, 1950), and others. Fabricius and Gustafson (1958) note that on the spawning grounds male northern pike often adopt a characteristic threat posture, with mouth slightly open and branchiostegal membranes lowered. In the present study, branchiostegal displays generally consisted of a sequence of these acts, with each successive act increasing in intensity. Fabricius and Gustafson (1958) also state that the displaying fish turns its flank towards the opponent, giving the threat posture the characteristic of a lateral display. In this study, the displayer was usually located in front of the recipient, but faced away on an angle. Thus it appears that, although the same morphological features are involved, the form of the spawning display differs from that given by post-spawning northern pike.

In form the branchiostegal display is similar to the gaping movements which follow consumption of prey. This display is also used following unsuccessful predatory attempts. In this context the display appears to serve as an outlet for a frustrated drive, but during intraspecific interactions it may have a secondarily aquired signal function. On the basis of criteria outlined by Blest (1961), it appears likely that this display has been derived from predatory gaping movements, and has undergone considerable ritualization. The form of the display is somewhat different from predatory gaping, in which the jaws and opercula are not opened simultaneously. Rhythmic repetition of the display occurs, and intensity is increased while speed of performance is decreased, resulting in exaggeration of the gaping movements. The fact that the display also occurs in the conflict situation of thwarted predation suggests that an incipient predatory drive plus an approach drive may be in conflict with escape tendencies during interactions with conspecifics. Keenleyside and Yamamoto (1962) conclude that the frontal display (gaping) in atlantic salmon indicates conflicting tendencies of escape, approach, and predation. The facing away orientation of northern pike during branchiostegal displays, which may indicate escape tendencies, exposes the bright red of the gills on a background of white directly toward the opponent. This feature may lend additional signal function to the display. Collias (1944) notes that bright colors are often emphasized in threat displays.

Branchiostegal displays were the form of threat most frequently employed during agonistic interactions (Table 22). Stokes (1962) states that animals rely on a small number of behaviors to confer their intentions to conspecifics. It seems likely that the branchiostegal display confers the intentions of an individual, since this display still retains superficial similarities to the activity from which it was apparently derived. Presumably, other northern pike can recognize the predatory components in these movements, and react accordingly. Baerends (1957) and Stokes (1962) agree that displays may be most effective when still supplied with information from instincts from which they were derived. Branchiostegal displays of northern pike still retain suggestions of predatory instincts. The singular, high importance of this display implies that degrees of aggressiveness are not an important feature of agonistic behavior in northern pike. This might be expected, since northern pike are not territorial, and Etkin (1967) notes that gradations in levels of threat decline with distance from the center of the home territory. In addition, it is known that ritualized displays develop a typical intensity, such that the form of the display remains constant over a wide range of intensities of eliciting stimuli (Hinde, 1966).

Snapping display

Snapping display has not been observed in previous studies of northern pike behavior. McNamara (1937) and

Fabricius and Gustafson (1958) do report the occurrence of actual nipping between males and females during spawning. This may indicate that at times of high sexual motivation the proximity of the mate is a stimulus of sufficient magnitued to elicit actual biting. In postspawning agonistic interactions the display is given at a distance from the recipient, so that biting never occurs. The display is never directed toward the recipient in the case, but occurs as the displayer moves across in front of the second fish. This may indicate that escape tendencies are inhibiting closer approach to the rival.

This display is virtually identical in form to the snapping employed during pursuit predation. When used as a threat display the only detectable difference between the display and its example is the lack of orientation towards the releasing stimulus. The basic predatory attributes are still strongly represented in this act. The display is also variable in its duration and intensity, which, according to Morris (1957), indicates little ritualization of the act has occurred. Because the act has not changed significantly in form from its example it seems plausible that it could be confused with a normal predatory act. Hinde (1966) postulates that displays which have changed little from their example are probably low in sign value.

Body wag display

Svardson (1948) reports male and female northern pike performing a synchronous "swimming standstill" during the mating act. He states that movements of all body fins increase until the bodies of the two fish vibrate in unison. The body wag display consists of swimming movements performed by a stationary fish, but certain aspects of the display are definitely different from those described by Svardson (1948). Firstly, the only paired fins used during the display are the pectorals, which beat forward, apparently counteracting any thrust produced by the caudal fin. Secondly, in the display the swimming movements of the trunk are performed slowly and smoothly, with no vibrating observed. Thirdly, the amplitude of caudal sweeps is greater than that noted by Svardson (1948). Fabricius and Gustafson (1958) suggest that the swimming standstill during mating is a modification of normal forward swimming caused by the confined space in Svardson's (1948) aquarium.

Body wag displays, of various degrees of similarity to those of northern pike, occur in numerous other families of teleosts. The display is used by: at least three genera of cichlids (Baerends and Baerends-Van Roon, 1950), Stichaeus (Farwell and Green, 1972), Aphyosemion (Ewing and Evans, 1973). The display also occurs in the genus Salmo, where it is usually associated with the presence of current, as in a stream (Keenleyside and Yamamoto, 1962; Chiszar et al., 1975).

For most species of fish it is presumed that this display has been derived from incipient swimming movements. For northern pike this may be partially true, but the form of the display is much more suggestive of the "S-posture" (Hoogland _et al._, 1956) adopted prior to a predatory strike at a stationary prey. The erection of pectoral fins appears to have functional value in the display, but Fabricius (1953) notes that this movement may be derived from braking maneuvers, indicating an increased escape tendency. Whether the fin erection has a sign value in northern pike is not certain, since this character is not emphasized because the displaying fish does not face directly toward the recipient.

Significant ritualization of the display has apparently occurred. Again this assumption is based on the criteria indicating ritualization (Blest, 1961). First, the intensity of the behavior has increased. Second, the movements are exaggerated. Third, rhythmic repetition is apparent. Fourth, the speed of performance has changed.

Belly flash display

Baerends and Baerends-Van Roon (1950) describe an activity, performed by cichlids, which is similar in form to the belly flash display of northern pike. They term this activity "chaffing", but note that it likely functions as a comfort movement. This is assumed because the activity by cichlids occurs in the absence of an external stimulus, and does not appear to have displacement qualities. Chaffing is also employed by atlantic salmon, but in this species it has the distinctive attributes of a displacement activity (Kalleberg, 1959). Kalleberg (1959) observed territory holders using this behavior when irritated by the presence of a conspecific. A displacement activity used in such cases can aquire a signal function through ritualization (Tinbergen, 1959). In cases where this display is used during interactions between northern pike, certain components of the act seem to be consistently oriented towards the recipient. This fact may suggest that in this species a degree of ritualization of the act has occurred.

During intraspecific interactions the displaying northern pike is always within the visual field of the recipient. The visible white flash, produced when the belly is presented, occurs directly in front of the opponent. The tendency to always present the ventral surface toward the recipient fish does suggest that some signal value is associated with the white flash produced (Collias, 1944). If this were not the case, it might be expected that the dorsal surface would have an equal probability of being presented to the recipient. From these findings it appears that the display may have more than a displacement function when used during interactions between northern pike.

Belly flash displays were only used twice by solitary northern pike, and the form of the act was identical to that occurring during interactions. The function of belly flash displays in these two situations is not clear. In fact, no basic activities were ever observed whose form suggested any relationship to the belly flash display. Baerends and Baerends-Van Roon (1950) suggest that the behavior pattern in cichlids may facilitate the removal of ectoparasites from the displayer's body. There is, however, no real evidence to suggest that this might also be the original reason for the behavior in northern pike. Additional examination of this particular behavior is required to determine its significance and origin in northern pike.

Head shake display

This display also occurs during spawning activities, when unripe female northern pike use it to repulse courting males (McNamara, 1937; Fabricius and Gustafson, 1958). It seems that the form of the display used in spawning differs from that used in agonistic interactions between post-spawning fish. Fabricius and Gustafson (1958) contend that the head is jerked quickly toward the opponent, and then returns to the midline. They also note that this behavior can be repeated several times, at intervals of some few seconds. In postspawning fish the head is swung rapidly from side to side during this display, with no pause between repetitions of the cycle.

Fabricius and Gustafson (1958) do note the striking similarity between this display and the prey turning movements employed by northern pike. In their description the display has a form identical to prey turning movements, in which the predator's head is jerked back only to the midline. In postspawning fish the display has two added components. A complete arc is described by the head, and the repetition occurs without interposed pauses. From this it seems that the postspawning display shows the greater degree of ritualization (Blest, 1961). The coordination of the activity has changed from that of the predatory behavior. The speed of the movements have increased. The head shaking has been exaggerated by increasing the amplitude and number of movements. There is rhythmic repetition evident in the display activity.

Gulping

It is not certain whether gulping activities have a definite display function. The action occurs at extremely low frequencies, and in addition it seems to lack any component of orientation in relation to the opponent. Northern pike are physostomes, thus it might be suggested that the act relates to adjustments of the gas content of the swim bladder. Bennet (1971) reports that under conditions of low oxygen or high carbon dioxide tension some species of fish will gulp air at the water surface.

If the gulping act performed by northern pike is purely a physiological response to enviornmental conditions, one may expect a higher frequency of occurrence of the act. Also, the act was never undertaken by a number of fish on the same day, as would be the case under conditions of low oxygen or high carbon dioxide. The features of the gulping act suggest that its function here is not basically physiological in nature.

Cichlid fishes carry on nipping movements at the water surface (Baerends and Baerends-Van Roon, 1950). These activities are especially employed by paired males at the end of breeding cycles, which implies that a display function is associated. For northern pike, the amount of available data is not sufficient to determine the possible function of the activity during interactions.

b. Nondisplay Agonistic Interactions

Interactions were also considered to be agonistic in nature if one individual exhibited avoidance behavior, even though no apparent threat display had occurred. Approach by a conspecific, at any speed, was often sufficient to elicit avoidance responses from northern pike. The frequency of occurrence of this kind of agonistic interaction was approximately equal to that of display interactions. Avoidance responses consist of slow movement, by one individual, away from the point of encounter. Occasionally this entails movement from open water into vegetation or vice versa. No particular submissive posture could be detected in the departing individual, but avoidance itself may be an indication of subordinance (Leyhausen, 1965).

Approach by another northern pike may provide the suggestion of intended aggression, and in some cases this alone is sufficient to elicit a response. Chiszar *et al*. (1975) find that rainbow trout (*Salmo gairdneri*), as they grow older, show increasing propensities to avoid an approaching individual, before an overt interaction occurs. These workers feel that the approach acts as a conditioning stimulus because of its constant association with attack, and in time approach itself aquires the ability to elicit an avoidance response. Sufficient data on the agonistic behavior of juvenile northern pike is not available to conclusively determine if such ontogeny of response occurs in this species. However, it is plausible that the tendency to react to approach could be an inherent trait of a species, which would obviate the necessity of social conditioning. From the brief comments on fry behavior made by Frost and Kipling (1967) it appears that juvenile northern pike also exhibit intraspecific avoidance. This does suggest that in northern pike the behavior is not totally a result of conditioning. In addition, it is possible that approach has certain attributes which are suggestive of incipient predatory movements, and it is known that juvenile northern pike show immediate avoidance reactions to potentially cannibalistic overtures of adults. The continued association of approach with cannibalism may be partially responsible for the avoidance responses of adults also.

The aptness of retreating fish to depart slowly may be functionally important in preventing pursuit by the approaching northern pike. Goldeye (Hiodon alsoides) which retreat slowly during aggressive interactions seldom elicit pursuit by conspecifics, while individuals showing rapid flight are often chased by the dominant (Fernet and Smith,1976). It has been shown that rapidly moving prey organisms, as opposed to slow moving prey, have a greater probability of releasing predatory acts by northern pike. If the predatory drive is partially involved in eliciting approach during intraspecific interactions, then slow retreat would be advantageous in preventing a hightening of this drive. The habit of juvenile northern pike to move slowly away from adults seems to function in exactly this manner. This basic mode of action in potentially cannibalistic interactions, although slightly modified in adults, may be partially responsible for the characteristic speed of retreat employed in agonistic interactions.

c. Quantitative Analysis of Agonistic Behavior

1973 and 1974 levels -

The mean level of activity displayed by northern pike in 1974 was twice as high as that of fish observed in 1973. This was the apparent cause of a higher mean interaction rate in the second year. At higher interaction rates it might be assumed that aggressiveness would be enhanced, particularly in a solitary species. However, agonistic behavior was manifest in a significantly smaller proportion of the interactions occurring in 1974. Data indicate that the difference can be largely attributed to the lower food availability experienced by the northern pike studied in 1973.

These findings illustrate the sensitivity of even social behaviors to environmental fluctuations in the wild. Information such as this points out the basic danger of describing the nature of a species from studies conducted under highly artificial conditions in which variability has been eliminated.

Male and female aggression

The aggressive tendencies of male and female northern pike, following spawning, were found to be similar. Only in nondisplay agonistic interactions in 1974 did males assume the position of subordinate significantly more often than females. Data indicate that this apparent disparity was a result of size differences between males and females, and not a result of any sex-related difference in aggressiveness. A similar condition exists for pumpkinseed sunfish (Lepomis gibbosus) in which females may assume the dominance position in a hierarchy, but this is only due to their larger body size (Erickson, 1967). Present findings do not support the assumption that female northern pike are necessarily more aggressive than males following the spawning run (Makowecki, 1973).

The pattern of similarity of behavior of male and female northern pike appears to hold throughout the summer months. There is, however, some suggestion from the literature that behaviors of males and females may diverge during the winter. Casselman and Harvey (1975) determined that mature female northern pike experience higher mortality due to low winter oxygen levels than do males of the same age. This they feel is due to higher metabolic activity of females during winter in relation to growth and gonadal development, which in turn is dependant upon feeding and related activity at that time. Hence, it may be suspected that sex-related differences in behavior could arise during the winter months. This does not necessarily imply that females would become increasingly intolerant of males at this time. Collias (1944) notes that increasing intolerance results in solitary habits, while Ivanova (1969) reports that actively feeding northern pike may aggregate in areas of high prey abundance.

Fish size and aggression

The relative size of a northern pike does not effect its tendency to display during interactions (Table 25). Similarly, this parameter does not effect the aptness of a fish to show avoidance once a display has occurred (Table 26). However, in nondisplay agonistic interactions the smaller of the two fish involved shows significantly greater avoidance tendencies. Allee and Dickinson (1954) report similar size related avoidance in nondisplay interactions between smooth dogfish (Mustelus canis).

Superficially, the presence of size related effects in nondisplay interactions seems to contradict their absence in display interactions. Several reasons may exist for these apparent inconsistencies of behavior. The first reason relates to display levels of different sized fish. In this species it is evident that only a few types of displays are used in agonistic situations. Stokes (1962) has shown that for certain species a single type of display is used over a wide range of aggressive tendencies. He concludes that displays, in such cases, are only a general indicator of underlying tendencies, and thus can not be expected to convey an absolute signal to a rival. This could suggest the reason for similarity of display levels in smaller and larger northern pike involved in interactions. For fish of two different sizes the same agonistic display may be employed, even though the relative levels of underlying aggressiveness may not be identical in both fish. Functionally, the act may have value to smaller and larger fish alike by transmitting information indicating that an individual space has been violated. The second reason for apparent inconsistencies in agonistic behavior relates to size associated avoidance in display and nondisplay agonistic interactions. It has been suggested that predatory tendancies are also shown during agonistic interactions between atlantic salmon (Keenleyside and Yamamoto, 1962), and it is assumed that this is also the case in northern pike. Approach alone may only convey the intentions of attack and predation (which may be very similar in appearance), and these are usually sufficient to cause avoidance when the approaching fish is larger. Support for this suggestion is gained from the work of Allee and Dickinson (1954). Conversely, a display, in addition to conveying the intention of attack and predation, also indicates the escape tendencies of the aggressor (Tinbergen, 1952; Hinde, 1966). Thus with a display an ambivalence is indicated, and the interaction takes on the form of an agonistic one rather than a purely predatory one. It may not be functionally necessary for a slightly smaller individual to show overt avoidance in such situations, where as in situations where a cannibalistic act is suggested, avoidance may be the expedient reaction for a smaller fish.

Such a pattern of agonistic behavior appears to be consistent with the social structure existing in northern pike populations, which is a system based largely upon individual distance requirements (Frost and Kipling, 1967). Marler (1956) contends that displays can indicate that an individual is aggressive, but is not willing to enter into a higher order interaction at the time. It is possible that displays of northern pike convey this same type of information, and that no extreme reaction by the recipient is required to allow individual distance to be maintained. It usually is evident that the displaying fish is not attempting to usurp the particular site occupied by the opponent, since it is most frequently the displayer who leaves the area of interaction. The impression gained is that the display only functions to indicate the tendencies of the displayer, and thus may act as a deterrent to any approach tendencies of the opponent.

Consistency of agonistic displays

The pattern of agonistic displays employed by northern pike did not change between 1973 and 1974, years with high and low levels of aggression respectively (Table 22). This finding further supports the view that the type of displays used can remain constant over a wide range of underlying aggressive tendencies (Stokes, 1962). Zack (1974) similarly finds that for Hermissenda an increase in the frequency of agonistic interactions does not grossly effect the pattern of displays employed. It does not appear that the various types of displays utilized by northern pike are brought into play to indicate different levels of aggressiveness. In addition, there appear to be no obvious relationships between the type of display employed and the particular circumstances under which it occurs. Northern pike displays appear to occur on an all or none basis, and the motivational state of the animals involved will determine if any display is given during a particular interaction. On the basis of data available, it is not obvious why the different display types should occur at characteristic frequencies relative to one another in two different populations of study fish.

Effects of agonistic displays

In addition to not occurring in any particular type of situation, the five kinds of agonistic displays used by northern pike do not appear to elicit different kinds of reactions from recipients. This implies the absence of specific levels of threat associated with each type of display.

Prolonged bouts of displaying are never observed to develop, and displaying fish leave the area of interaction significantly more often than recipients (Table 20). From this it follows that classical requirements of territory or position in a dominance hierarchy are not being disputed.

Again, the only plausible function of agonistic displaying seems to be the reduction of violations of an individual's critical space when its tolerance is low.

An indication of the range of social tolerance in northern pike is gained from the fact that in both years of the study a small percent of display interactions resulted in mutual activity between the displayer and recipient. In none of these cases was aggression shown during the subsequent mutual activity. The frequency of occurrence of this particular type of behavior was sufficiently low to suggest that it may result only in rare cases where intentions are not clearly transmitted or recieved.

3. Positive Interactions

Northern pike are often described as solitary fish (Wich, 1958; Nursall, 1973), and on the basis of the behavior observed, this description seems correct. Breder (1959) defines solitary fish as those "showing zero or less attraction towards others of their kind." This definition is not applicable to northern pike, unless provision is made to allow for low intensity, facultative, positive interactions. These fish on occasion do display appetence for and enter into intraspecific interactions, which seem to have a mutually positive value for the participants. Thus present observations can not substantiate those of Frost and Kipling

(1967), which indicate that northern pike always avoid one another. Leyhausen (1965) describes positive interactions between free ranging cats, which are normally aggressive towards one another. He concludes that such behaviors, even in a solitary species, arise from an urge for social togetherness. The occurrence and acceptance of body contact between northern pike in these interactions suggests that the normal individual distance requirements of participants have been temporarily deferred. Presumably this indicates that both individuals derive benefit from the activity. The work of Bartman (1973), although not dealing with intraspecific interactions, does indicate that northern pike will suppress basic drives to obtain a beneficial result. He reports the existence of a cleaning symbiosis between northern pike and Gasterosteus . It seems that in this case the benefits of ectoparasite removal have been accepted in lieu of a predatory act on the potential prey. The suppression of aggressive tendencies during positive interactions between northern pike must similarly be stimulated by positive attributes of the activity.

4. Social Structure

The social structure of northern pike populations is a composite of various components of dominance hierarchies, territoriality, and home range; superimposed on these components is the system of individual distance requirements. No single theory of population social structure seems to adequately describe the system employed.

Dominance relationships

The pattern of hierarchical relationships in northern pike populations appears to depend solely upon size related avoidance behavior. The behavior shown by the smaller fish involved in a nondisplay agonistic interaction implies that this avoidance is largely dependent upon reactions to the predatory attributes of approach. Agonistic displays alone do not possess the potential for stimulating the development of a hierarchy in this species. Hoar (1951) similarly finds that aggression in coho salmon (Oncorhynchus kisutch) populations produces no dominance hierarchy. Since social dominance through aggression does not seem to be important in this case the term avoidance hierarchy may be more appropriate.

The unique relationship which developed between fish JP1 and MP1 may also have been contingent upon the relative sizes of these two individuals (Figures 20, 21, 22). As a result of the almost complete overlap of the areas frequented, the presence of MP1 may have abnormally suppressed the activity of JP1. This could explain the change in behavior of JP1 when MP1 was removed, without requiring the assumption of existence of individual recognition. Although individual recognition could exist, it does not seem likely that this ability is a normal requirement of a solitary fish. It may also be postulated that such a relationship would not persist for an extended period in the wild.

Site use

"Territories are particular areas occupied and defended by particular individuals" (Erickson, 1967). Although northern pike do at times show preferences for particular restricted sites, these areas are never defended. Thus present observations can not support the suggestions of territoriality in northern pike (Svardson, 1948; Makowecki, 1973).

Temporary sites used by northern pike are always associated with environmentsl reference points, such as aquatic vegetation beds, submerged logs, over-hanging trees, etc.. Kalleberg (1959) similarly finds that the home sites of atlantic salmon and brown trout are always associated with specific physical structures in the enviornment. Kalleberg (1959) and Hartman (1965) agree that increasing the number and diversity of reference points, as visual isolation is increased, allows for increases in the population density of a solitary species. Visual isolation also seems to be an attribute of the temporary sites of northern pike. The association between JP1 and MP1 illustrates how visual isolation can function to reduce potentially harmful interactions. Individual northern pike show extreme variability in duration of attachment to a particular temporary site. Ewing and Evans (1973) find that *Aphyosemion* (Rivulini) shows similar attachment to preferred sites, but that the attachment changes over a period of a few days. Temporary site attachments are not essential, in most cases, for stability in northern pike populations. This is inferred from the abrupt manner in which site attachments were initiated and terminated, as in the case of fish C (Figure 23). Also, during temporary site attachment individuals did use other portions of the available area. Predatory activities of site holders were carried on in all portions of the observation area, indicating that the particular sites which were held did not function primarily as feeding stations, as is often the case in territorial birds (Tinbergen, 1957).

The reactions of site holders to the presence of an interloper in the resident's own site was seldom aggressive. Aggression might be expected if a site was an area giving the resident priority of access to certain resources (Collias, 1944). Leyhausen (1965) reports that superior cats will not normally drive away an inferior one which is already occupying the superior's favorite resting place or lookout post. He further notes that both superior and inferior cats occasionally freely trespass in the other's home area, when the resident is present. This situation is virtually identical to that occurring during temporary site attachment by northern pike. It appears that the temporary site of northern pike functions largely as a resting site, which is ephemeral in its popularity.

The importance of temporary site should not be over emphasized, since it is an infrequent and unstable phenomenon. Generally, most fish do not show a particular pattern of site use. Any area of suitable habitat with vegetational cover seems to be acceptable as a resting spot in most cases.

Range

Northern pike do exhibit restriction of their range of travel. This is concluded from the restricted pattern of use of available space shown by fish held in the observation channel (Table 30). Tagging studies indicate that this pattern also exists in the wild for periods of more than one year (Makowecki, 1973). Makowecki (1973) indicates that this habit may develop through the continued use of areas of superior habitat. This may suggest the existence of home range habits in northern pike populations. Gerking (1953) defines home range as "the area over which an animal frequently travels." Northern pike do not show a tendency to regularly patrol specific areas. The fish did largely restrict their activity to the lower portion of the observation area, but movement within that area showed no consistent pattern from day to day. Overlap and simultaneous use of areas does occur as a result. The data indicate that these fish will confine their activity to large areas of preferred habitat, but that excursions in the area follow no particular home range pattern. Northern pike are evidently flexible in all these requirements, adjusting their activities to suit the environmental and ecological conditions encountered.

Rates of travel of northern pike varied from day to day, and also showed differences between the two years. Average distances of travel, from observations, varied between 0.1 and 0.2 km per day. Such values agree well with the calculations of Malinin (1969). He determined the daily range of northern pike to be an area approximately 50 to 150 meters in diameter.

Individual distance

Superimposed upon the partial systems of hierarchy, territory, and home range use is the pattern of individual distance requirements of northern pike. Frost and Kipling

(1967) first detected this need in juvenile northern pike held in aquaria. They conclude that individuals require an unviolated space around themselves, which if denied will result in aggression. Present findings confirm that individual distance is a requirement of northern pike, but that these requirements are possibly more dynamic than suggested by Frost and Kipling (1967). Marler (1956) describes the measurable individual distance requirements of chaffinches (Fringilla coelebs), and notes that these too are subject to change. For northern pike, the model of individual elastic spheres of territory around each fish appears to apply well. These spheres are compressible and inflatable with changes in a number of variables. First, when the size differential between two fish is great the smaller fish will likely show the greatest individual distance requirement. This functions to insure that the smaller fish will have a reduced chance of entering into a harmful interaction. Second, at times of low food availability (1973) individual distance requirements increase. This may operate as a mechanism to facilitate efficient spacing of individuals, and also as a means of reducing aggressive interactions related to a high predatory drive. Third, when food is abundant and concentrated, individual distance requirements may be reduced, allowing the predators to congregate and exploit a temporarily available resource (Ivanova, 1969). Fourth, during positive interactions individual distance requirements may be temporarily deferred to allow actual physical contact between individuals.

In the natural environment visual isolation, afforded by physical barriers, is apparently sufficient to fulfill an exceptionally large individual distance requirement.

During the study northern pike preferentially frequented the lower portion of the observation channel (Table 30). Even in 1973 when levels of aggression were highest the fish did not space themselves out evenly within the available area. Free ranging, solitary cats show a similar tendency to remain nearer to one another than would be expected, even when there is no apparent reason to do so (Leyhausen, 1965). Wynne-Edwards (1962) and others have suggested that for many species there is not only a minimum but also a maximum size of territory (individual distance in this case). In northern pike populations too there apparently exist certain centripedal social forces, which operate antagonistically to the more obvious repulsive forces. The point at which these mutually opposed forces are balanced should be the normal separation distance between individuals.

D. 1973 vs 1974: Activity, Aggression, and Predation

RESULTS

Consistent differences in the levels of activity and aggression existed between the 1973 and 1974 populations of northern pike held in the observation area. In an attempt to account for this disparity a number of environmental and population parameters were compared for the two populations. An examination of the results of these analyses, and the proposal of a theoretical model to account for the observed differences follows. It must be emphatically stated that the theory proposed represents only one possible explanation, and that data from more highly controlled experiments may be required before definite conclusions can be drawn.

Activity and aggression 1973 and 1974

The average activity levels of northern pike were twice as high in 1974 as in 1973 (Table 32). The times of day at which observations were conducted were similar in both years. The diurnal activity rhythm of fish observed (Figure 15) showed a high positive correlation between the two summers ($r = +0.85$). This suggests that the activity levels extant during both summers were normal, since they did occur within the framework of the typical daily activity cycle.

The relationship between density of northern pike in the observation area and levels of activity was opposite for the

Table 32. Summary of data examined in relation to the behavioral differences existing between 1973 and 1974 study fish populations.

Category and aspect examined	1973	1974	Statistical relation
Activity			
1. average % active/fish	19.8%	40.8%	
2. correlation diurnal cycles 1973 and 1974			+0.85
3. correlation activity and fish numbers	r= -0.91	r= +0.74	
Interactions			
1. interactions/hour/fish	0.98	1.68	
2. % agonistic display	30.5%	9.7%	1973>>1974
3. % nondisplay agonistic	30.5%	9.8%	1973>>1974
4. % neutral	22.7%	62.8%	1973<<1974
5. % positive or cohesive	16.3%	17.7%	1973=1974
Environmental correlations and observations			
1. activity and mean weekly water temperatures	r= -0.26	r= +0.09	N.S.
2. activity and barometric pressure (daily)	r= -0.36	r= -0.17	N.S.
3. activity and absolute change of b.p.	r= +0.04	r= +0.26	N.S.
Environmental correlations and netting data			
1. correlation % of sample feeding and mean weekly water temperature	r= -0.08	r= -0.17	N.S.
2. correlation % of sample feeding and barometric pressure	Combined	r= +0.22	N.S.
3. fish/standard net gang and absolute change in b.p.	Combined	r= -0.18	N.S.

Table 32. continued

Category and aspect examined	1973	1974	Statistical relation
Predation			
1. prey fish added	160	550	
2. prey ration / predator/day	0.47	1.22	
3. predatory acts observed	14	98	
4. predatory acts/hour/fish	0.036	0.14	

Chi Square significance indicated by < at 5% level and << at 1% level. Nonsignificance indicated by =.

Nonsignificant correlation coefficients (less than ±0.70) indicated by N.S..

two years of the study. In 1973 activity levels showed a high negative correlation with the numbers of fish in the observation area ($r = -0.91$). In 1974 the opposite situation existed, with activity being positively correlated with numbers of fish ($r = +0.74$). Similar numbers of fish were held in the observation area in both years. Also, no difference in the type or amount of habitat available existed between the two years. The activity anomaly could be produced in two ways. Northern pike in 1973 may have exhibited higher avoidance of conspecifics, and therefore reduced activities in response to increased density. Conversely, in 1974 a form of social facilitation may have been operating, which caused activity to be enhanced at higher densities.

Higher intraspecific interaction rates were also apparent in 1974. The levels were 0.97 interactions/hour/fish in 1973, and 1.68 interactions/hour/fish in 1974 (Table 32). These levels appear to be what one would expect as a result of the increased activity in the second year. However, the type of behavior employed by fish during interactions in each year was not simply a result of increased activity. In 1973, 22.69% of the interactions were of the neutral variety, while in 1974, 62.76% of the interactions were of this type (Table 32). The observed level of neutral interactions was significantly higher in 1974 than in 1973 ($p<0.01$). The level of agonistic interactions, both display and nondisplay, was approximately three times higher in 1973 than in 1974

($p<0.01$). The mutual or positive interaction levels were almost identical for the two years. Although fish were more active and had a higher interaction rate in 1974, the level of aggression was much lower than in 1973. It appeared that in the 1974 population northern pike tolerated the presence of conspecifics to a greater degree than in the 1973 population. One might infer from these data that the level of aggressiveness existing in the 1973 stock tended to suppress fish activity. This would appear to explain the density dependent reduction in activity observed in that year. Conversely, in 1974 with lower intraspecific aggression, fish activity was not suppressed, since fewer interactions were of a conflict nature. The density-related rise in activity in 1974 may have been a result of a form of social facilitation, but this is not certain. The similarity in the levels of mutual social interactions suggest that a certain background level of social cohesiveness naturally exists in northern pike populations.

The problem which remains is to determine what factor or factors could have been responsible for the differences in the behavior of the two groups of fish.

1. Environmental Factors

The semi-natural situation in which northern pike were observed allowed the fish to be subject to normal environmental fluctuations. Hence it is important to determine what effect these variables have on the behavior of northern pike, and whether any gross environmental differences existed between 1973 and 1974.

Dissolved oxygen levels were similar in both years, with the mean level in the observation area being 7.17 ppm in 1973 and 7.32 ppm in 1974. The lowest values occurred each year in June, and were 5.60 ppm in 1973 and 5.20 ppm in 1974. All levels were within the tolerance limits of northern pike. Oxygen levels do not appear to be a critical factor, in this case, which could explain the behavioral differences observed.

Mean weekly temperatures were compared with the levels of activity observed. The correlations in both years were low and nonsignificant (Table 32). From netting data it was possible to examine the effect of water temperature on feeding in the lake population of northern pike (Figures 25 and 26). In both years the correlations between water temperature and feeding were low, and indicated no significant relationship between these parameters which could explain the behavioral differences observed. In addition, it is apparent that water temperatures followed a similar pattern in both

Figure 25. Frequency of occurrence of empty stomachs in netted northern pike in 1973, and relationship to mean weekly lake temperature. Correlation between mean weekly lake temperature and percent of stomachs empty is -0.076.

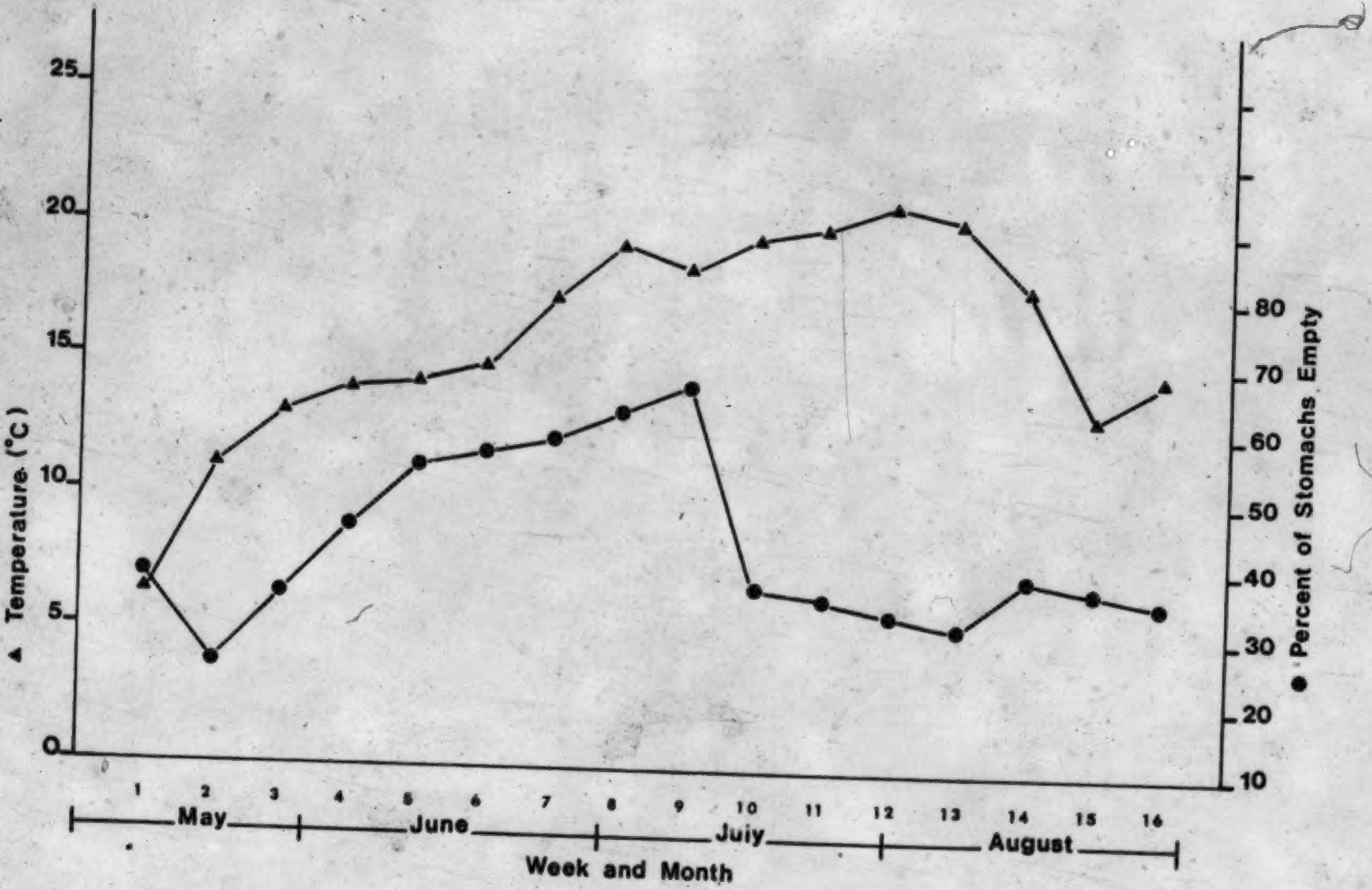
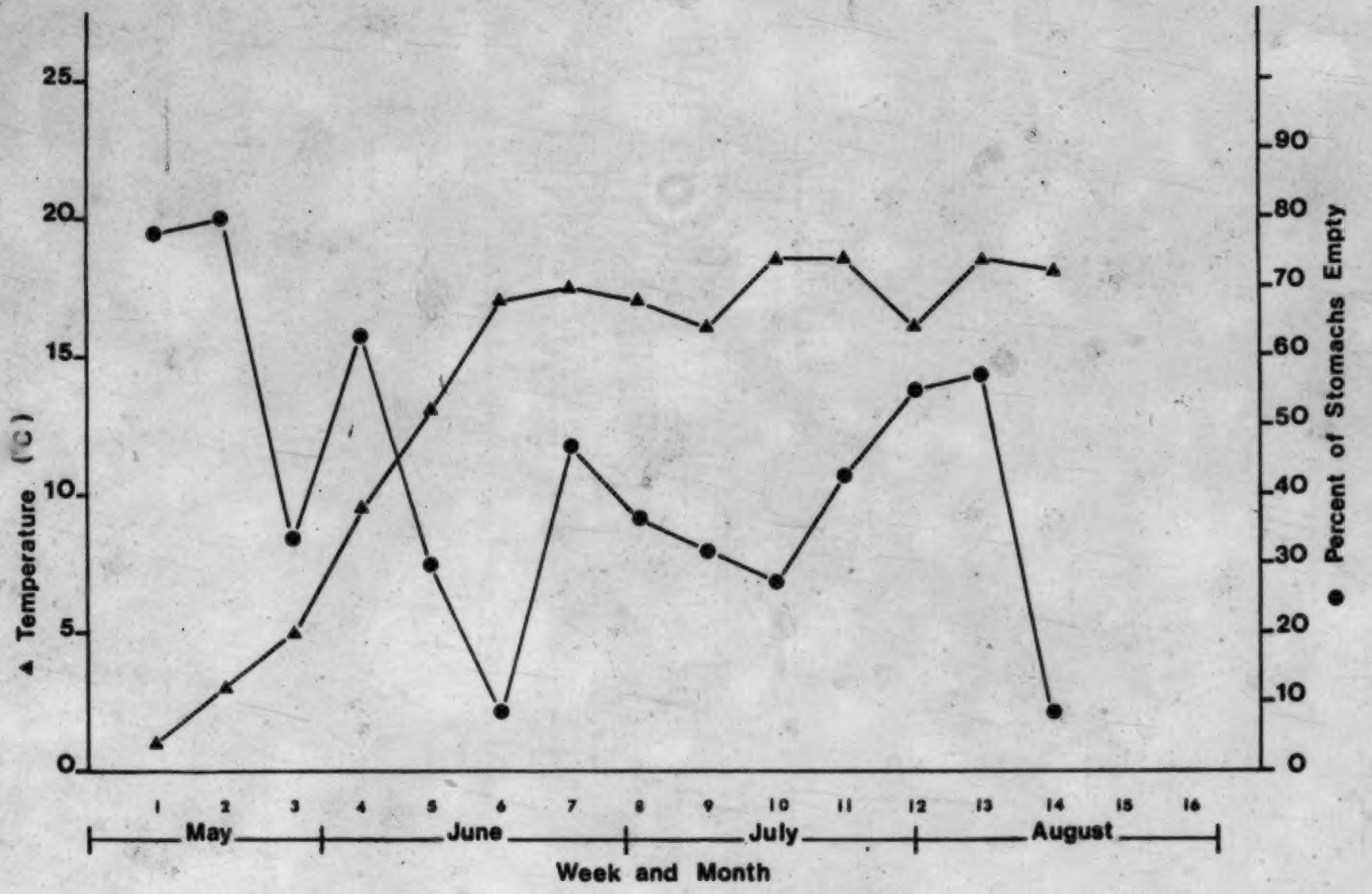


Figure 26. Frequency of occurrence of empty stomachs in netted northern pike in 1974, and relationship to mean weekly lake temperature. Correlation between mean weekly lake temperature and percent of stomachs empty is -0.17.



years of the study (Figures 25 and 26).

Malinin (1971) reports movements of northern pike to deeper water up to 24 hours in advance of sharp changes in wind direction and intensity. Barometric pressure changes may be involved in triggering these fish movements, so this parameter was examined in relation to the observed differences (Table 32). Comparison of barometric pressures on the day of observation with the observed activity level yielded a low negative and nonsignificant correlation in both years. Comparison of activity to the absolute, relative change in barometric pressure from the previous day yielded low positive and nonsignificant correlations in both years. To obtain information of the effects of barometric pressure on natural populations, standard net catches from both years were combined and a correlation analysis run. Fish numbers per standard test net showed a low negative and nonsignificant correlation with the absolute change in barometric pressure from the previous day. The feeding of net-caught fish showed a low positive but nonsignificant correlation with the absolute change in barometric pressure. It seems that the pattern and magnitude of changes in northern pike behavior caused by barometric pressure are not adequate to explain the behavioral differences recorded.

Environmental parameters do undoubtedly influence the general behavior patterns of northern pike, but the trends do not appear to be strong for those factors examined. Also, no clear, unidirectional trends in weather patterns could be detected in either year. This kind of information does not seem to adequately answer the activity and behavior problem.

2. Predation

The major remaining variable, and one that appears to explain a portion of the observed differences, is the level of predation occurring in the observation area in each year. In 1973, 160 prey fish were introduced into the observation area over the summer. In 1974, 550 prey fish were introduced over the summer. These numbers gave a ration of 0.47 prey/day/fish and 1.22 prey/day/fish in 1973 and 1974 respectively. The fate of all prey fish introduced could not be determined due to the nature of the observation area. The number of predatory acts observed does give an indication of the availability of food, if one assumes that the predatory drive remained fairly constant. In 1973, 14 predatory attempts were observed (0.036 acts/hour/fish); in 1974, 98 predatory attempts were observed (0.14 acts/hour/fish). The ration in 1974 was approximately 2.6 times higher than in 1973, which seems to agree reasonably well with the predatory act rate which was 3.9 times higher in 1974 than in 1973.

Using the 1974 data a comparison was made between days with and without predatory acts occurring. Six fish were examined over two, six day periods, with the display rates being compared (Table 33). The fish gave agonistic displays in 4.7% of their interactions on the days with no predation, and in 2.6% of their interactions on the days with predation occurring. The difference between the mean display rates observed during the two periods approaches significance at the 5% level ($p<0.07$). The observed differences might have been greater if these features could have been examined over a longer time period. In addition, it is possible that these tendencies develop over an extended period of high or low food availability, as in the two whole summers of the study. The work of Slaney and Northcote (1974) with rainbow trout shows that levels of aggression in confined populations display an inverse correlation with prey abundance. They also note that when fish are switched from high to low prey abundance situations or vice versa a lag period ensues before levels of aggression show a corresponding change. For opportunistic predators, such as northern pike which frequently undergo extended periods of fasting, this lag period could be of considerable length.

Table 33. Comparison of the display rates of six northern pike during a period of six days with no predation occurring, and six days with predation occurring. The values given represent the percent of interactions in which agonistic displays took place.

	Agonistic display rate of fish							
	D	C	E	B	F	G	Sum	Mean
No Predation occurring	5.0	4.4	8.3	3.4	6.1	1.0	28.2	4.7
Predation occurring	2.3	5.9	3.4	0.0	4.4	0.0	16.0	2.7

	5%	1%
t for 5 DF	2.571	4.032

Sample mean difference = 2.03
Standard error of the mean difference = 0.898

t = 2.32*

* t is significant at the 7% level.

DISCUSSION

These data, although not totally conclusive, do suggest a possible model outlining the relationships of feeding, activity, and agonistic behavior in northern pike. Data are not available to test these relationships over a wide range of food availabilities, but information obtained from the two summers of research may represent the situation at two points along a continuum. Figures 27 and 28 suggest a theoretical explanation for the situation observed.

Figure 27 illustrates the suggested relationship between predation, activity, and predator numbers (density). The 1973 data would represent the period of low predation on the graph. That year showed an inverse relationship between numbers and activity, which would parallel the decrease in activity shown. The 1974 data would represent the period of higher predation. The positive correlation between numbers and activity in that year parallels the rise in activity shown at high predation on the graph. The region of moderate predation levels on the graph is approximated, since data for this region are unavailable.

Figure 28 illustrates the relationship between predation, activity, and agonistic behavior. From Figure 27 the activity-predation relationship is suggested. Agonistic behavior levels in 1973 and 1974 would represent the high and low points respectively on this line showing the relationship between predation and agonistic behavior. This is further substantiated by the relationship shown in Table 33, where agonistic behavior was found to be higher at lower predation levels in the same fish in 1974.

The information obtained suggests that northern pike tend to become more aggressive in times of extended food shortage, and that this is accompanied by a decrease in activity. Conversely, at higher prey availabilities aggression decreases and activity rises. This would appear to be adaptively significant in two general ways. Firstly, northern pike would conserve metabolic energy by reducing locomotory activity, and because of this the species could endure extended periods of low food availability. The significance of this attribute comes to light when one considers the findings of Brett (1970). He states that during a brief burst of activity the energy expenditure may rise to 100 times the level in a resting fish. Johnson's (1966a) findings tend to agree with those of the present study, since she found northern pike to be active only in relation to actual feeding. She also states: "Pike, therefore, seems to be outstanding amongst those species studied, for its relatively low maintenance requirements, and relatively high rate at which it converts food to body-substance." This tendency to keep activity to a minimum appears to be a basic component of the overall predatory strategy of this species.

Secondly, by reducing activity at low prey availabilities northern pike would also reduce the frequency of intraspecific interactions, a higher proportion of which are agonistic under these conditions. The effect of conflict situations on the physiology of organisms has been well documented. Erickson (1967) reports an inverse correlation between the amount of interrenal tissue and the position of pumkinseed sunfish in a social hierarchy. Selye (1949, 1961) notes that the stress-caused collapse of the pituitary-adrenal system often seems to be the ultimate cause of death in conflict situations. Lockie (1956) finds more fighting in flocks of rooks (Corvus frugilegus) during cold weather when food is apparently in short supply. He speculates that submissive individuals would be more often displaced from food by frequent fights, and would subsequently starve. Findings from the present study suggest that within certain ranges of density and food deprivation, northern pike may limit their activity, with the result of keeping stressful interactions to a minimum. The work of Ivanova (1969) strongly supports this theory. She finds that in years of high prey abundance, northern pike in the Rybinsk Reservoir form temporary feeding aggregations on the spawning grounds of prey fish. In years of low prey availability, she finds that northern pike feeding is light, and individuals tend to be solitary in their habits.

It is possible that at higher prey availabilities the predatory drive is satisfied more frequently, thereby causing an associated lowering of the propensity for aggression. At lower prey availabilities the predatory drive is thwarted, and this drive may surface during interactions, where it could be combined with aggressive tendencies, causing a higher than normal display of agonistic behavior. If, however, within a certain range of food deprivation the hunting drive can be suppressed, the chances of entering into unrewarding, stressful interactions would be reduced. It is significant to note that most of the agonistic displays of northern pike appear to originate from basic predatory movements, suggesting that predatory drive is an underlying component of agonistic activities.

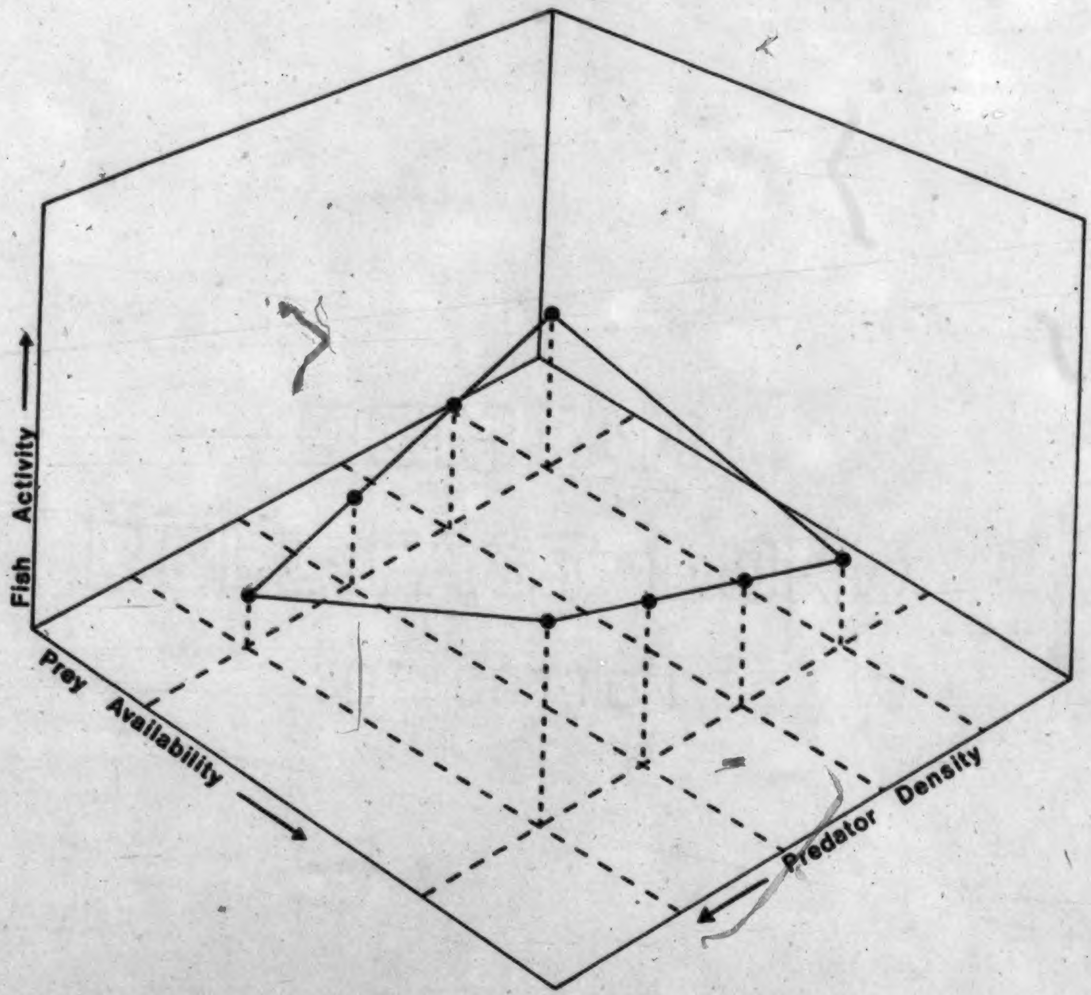

Fish Activity
Prey Availability
Predator Density

Figure 27. Suggested theoretical relationship between activity, density, and prey availability for northern pike observed.

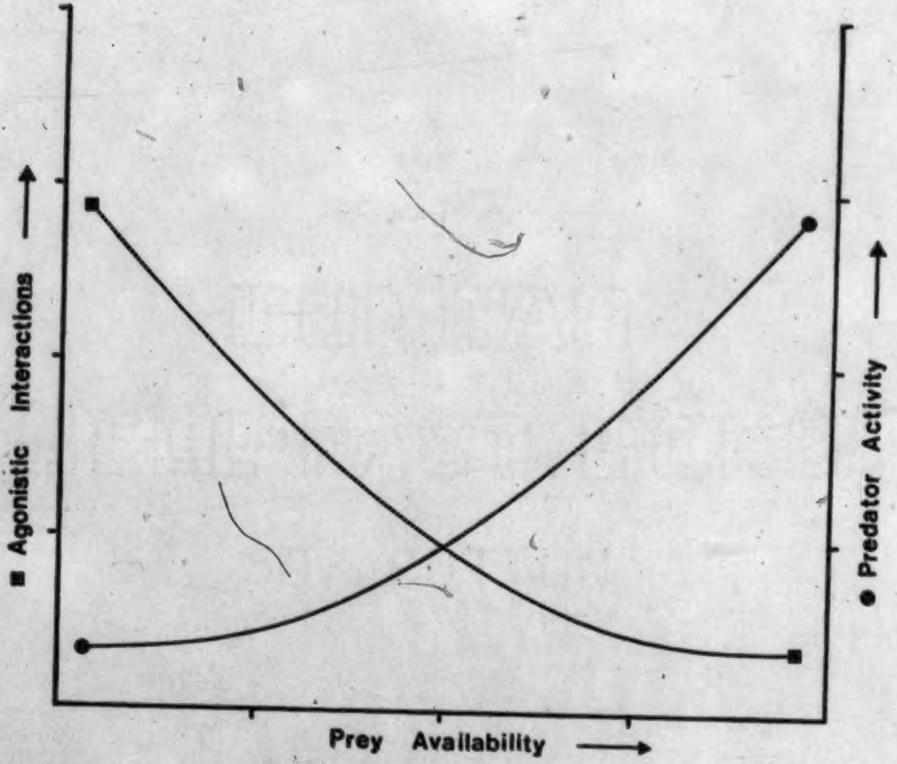


Figure 28. Suggested theoretical relationship between activity, agonistic interactions, and prey availability for northern pike observed.

SUMMARY

1. The average growth rate of Kakisa Lake northern pike is higher than that reported for other populations of this species from the same general area. The relatively high summer water temperatures and longer than average open water period of Kakisa Lake may be partially responsible for this situation.

2. Divergence in growth rate of male and female northern pike becomes apparent only after individuals attain sexual maturity. This fact suggests that physiological and/or behavioral changes associated with maturation are responsible for the observed sexual dimorphism in body size of northern pike.

The sexual dimorphism of jaw width in northern pike allows females to consume relatively larger prey than males of the same fork length. The higher efficiency of predation, thus attained, would contribute to the higher average growth rate of mature females.

The separation of preferred prey size, for male and female northern pike of the same fork length, must broaden the resource base utilized by the species, and also decrease competition between the sexes. Such factors should increase the carrying capacity of an environment for this species above that expected if no sex-related separation in prey size preferences existed.

3. In Kakisa Lake, mature northern pike display a distinct spawning fast. This behavior must function in reducing cannibalism during spawning, and also by insuring that reproductive activities occur at the optimal time.

4. The species composition of the diet of northern pike is partly determined by relative abundance of prey fish, and both seasonal and annual alterations in prey abundance result in diet composition changes. In addition, the diet of northern pike from different lakes can lack similarity, even though the prey species composition in the lakes may be virtually identical. The differences in habits of prey species, as related to lake morphometry and available habitat in each lake, appear to explain the disparity in utilization of certain prey species by different northern pike populations.

Northern pike in Kakisa Lake do consume disproportionately low numbers of spottail shiners and northern pike, and disproportionately high numbers of walleye. This is mainly a result of the particular behaviors exhibited by each of these three prey species.

5. Northern pike are size selective predators. With increase in body size of the predator feeding acts become energetically more costly, and to maintain a high predatory efficiency larger predators must consume relatively larger prey. The effect of size selective predation is reflected in disparities in species composition of the diet between the various size classes of northern pike.

6. Northern pike typically display minimal activity during the daylight hours, largely resorting to extended periods of inactivity. Such habits should result in substantial conservation of metabolic energy.

Cruising activity does not appear to be elicited by specific stimuli in all cases, while higher speed swimming is usually associated with specific external stimuli. A diurnal and seasonal cycle of activity exist, and both appear dependent upon light as a Zeitgeber.

7. Northern pike display a tendency to restrict most activity to areas of cover during the day, while areas of open water are avoided. Cover is essential for predatory success and also for reducing visual contact between northern pike.

Areas of vegetation and cover are preferred by northern pike as sites of inactivity.

8. Two modes of predation are employed by northern pike; stalking and pursuit, the occurrence of each is contingent upon the behavior of prey fish. Northern pike are most successful when employing stalking predation, which is largely dependent upon the ability of the predator to remain concealed prior to the predatory act. Thus, areas of abundant aquatic vegetation and cover are essential for efficient predation, and the related success of this species.

9. The general feeding strategy of northern pike is one of opportunistic use of temporarily available prey. Such a strategy is made possible by the ability of this predator to sustain extended periods of food deprivation without undergoing excessive physical deterioration.

The outcome of a predatory act dictates the pattern of behavior which will follow. Success of predation stimulates a brief period of increased appetitive hunting behavior, while failure of predation or rejection of prey inhibits intensified searching in the area of prey encounter.

10. In clear waters detection of prey is mediated by vision only, if the predator is between four meters to 15 cm distance from the prey. Within a distance of 15 cm prey detection depends on either visual or mechanical stimuli, but appropriate visual stimuli are

required before a predatory lunge is released in clear water. Under turbid conditions, when vision of northern pike is naturally impaired, detection and consumption of prey, with in 15 cm distance, is likely dependent upon mechanical stimuli, and possibly olfactory stimuli if prey is stationary.

11. A prey fish which is swimming rapidly and abnormally has a greater potential for releasing the predatory act of northern pike, than a prey fish which is moving more slowly in a regular manner. Inactivity of a prey fish can allow it to escape predation of northern pike in some cases.

12. Integrated schooling behaviors of certain prey fish species operate as deterrents to northern pike predation.

Northern pike possess the ability to visually recognise some prey species, and this likely develops by the conditioning effect of previous encounters with the particular species. This ability is evident in the reaction of northern pike to walleye.

Juvenile northern pike display the greatest diversity and most effective means of avoiding predatory attempts of adult northern pike.

13. Northern pike can recognize predatory behaviors of conspecifics, and are often stimulated to perform similar activities by observing other individuals engaged in such behaviors. Apparently, a form of social facilitation operates in these instances.

14. Juvenile northern pike display predatory behaviors which are similar to those of adults, but which lack the rigidity of form and skill characteristic of the adult behaviors. The lack of overt predator avoidance shown by juvenile prey fish allows young northern pike to attain a predatory success rate comparable to that of adults. Predatory behavior of northern pike undergoes an ontogeny, from juvenile to adult form, with accumulation of predatory experience.

15. Northern pike are basically solitary in their habits, but intraspecific interactions do occur, and their form can be neutral, agonistic, or positive. The solitary nature of the species may be temporarily deferred when aggregations of the predator form in areas of prey abundance, and also during positive intraspecific interactions.

16. Neutral interactions between northern pike are contingent upon mutual tolerance being shown by both participants.

Agonistic behavior of northern pike has two forms; these are simple avoidance and aggressive displaying. Avoidance is chiefly dependent upon the size differential between the opponents, with the smaller fish exhibiting significantly greater avoidance tendencies. The propensity of northern pike to display during agonistic interactions is not affected by the size of a fish relative to the opponent. Relative size does not affect the behavior of a fish following the occurrence of an agonistic display.

17. Most agonistic displays used by northern pike have the form of ritualized predatory movements, which indicates that the predatory drive is also an underlying component of aggressive behavior in this species. The different types of displays do not represent different levels of threat. However, approach may suggest predatory intentions only, and thus causes a more extreme response from an opponent than if an aggressive display, which also indicates escape tendencies, is employed during the interaction.

There is no basic, sex-related disparity in levels of aggressiveness of northern pike during the post-spawning season.

Physical combat is not characteristic of aggressive interactions between northern pike.

18. The aggressive behavior of northern pike is functional in maintaining individual distances between conspecifics. In most cases the aggressor does not attempt to drive the opponent away from a specific area, indicating that a territory is not being contested. Visual isolation, provided by physical structures in the environment, is important in maintaining aggressiveness at low levels in natural populations of northern pike.

19. Centripetal social forces also exist in northern pike populations, and these forces account for the uneven spacing of individuals throughout the available habitat.

During postspawning encounters between northern pike, positive interactions do arise, and these appear to have mutually beneficial value to the participants.

20. The social structure of northern pike populations is largely based upon fluctuating individual distance requirements. Aggressive displaying does not possess the potential of producing dominance hierarchical patterns, but nondisplay agonistic interactions do produce an unstable, size-related, avoidance hierarchy.

Northern pike are not territorial, in the classical sense, but they do infrequently develop temporary attachments to sites which are not defended. Range restriction, to areas of preferred habitat, is characteristic of this species, however, patterns of regular home range patrolling do not occur.

Individual distance requirements are largely satisfied by avoidance of conspecifics. Fluctuations in resource availability are reflected in corresponding alterations of individual distance requirements.

21. Increased prey availability appears to produce increased activity, increased social tolerance, and decreased aggressiveness in northern pike. Conversely, food shortages appear to induce decreases in activity and social tolerance, while aggressiveness rises.

Such a pattern of behaviors seems to have definite functional value. At times of high food availability northern pike can congregate to exploit the abundant resource. With increased predatory activity intraspecific interactions become more frequent, but because tolerance is high few interactions are stressful. Under conditions of food deprivation, increased aggressiveness would insure efficient spacing of individuals, while at the same time causing individuals to restrict activity. The resultant reduction in the rate at which metabolic reserves were utilized allows the predator to weather an extended period of low food availability.

22. The overall strategy of northern pike behavior is directed toward minimizing metabolic energy expenditure. This is achieved through maintaining activity at low levels, carrying out efficient, opportunistic predatory acts, and avoiding social strife.

LITERATURE CITED

Allee, W.C. 1951. Cooperation among animals. Rev. ed. Henry Schuman, New York, N.Y. 219 p.

Allee, W.C., and J.C. Dickinson, Jr. 1954. Dominance and subordination in the smooth dogfish (*Mustelus canis* (Mitchill)). Physiol. Zool. 27:356-364.

Allen, K.R. 1939. A note on the food of pike (*Esox lucius* L.) in Windermere. J. Anim. Ecol. 8:72-75.

Baerends, G.P. 1957. The ethological analysis of fish behavior, p. 229-269. *In* M.E. Brown [ed.] The physiology of fishes. Academic Press, Inc., New York, N.Y.

Baerends, G.P., and J.M. Baerends-van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. Behaviour Suppl. 1:1-242.

Baerends, G.P., R. Brouwer, and H.Tj. Waterbolk. 1955. Ethological studies on *Lebistes reticulatus* (Peters): I. An analysis of the male courtship pattern. Behaviour 8:249-334.

Bartman, W. 1973. A cleaning symbiosis between stickleback (*Gasterosteus aculeatus* L.) and pike (*Esox lucius* L.) in the aquarium. Z. Tierpsychol. 33:153-162.

Bennet, G.W. 1971. Management of lakes and ponds. Van Nostrand Reinhold, Ltd., Toronto, Ontario. 375 p.

Beukema, J.J. 1970. Aquired hook avoidance in pike (*Esox lucius* L.) fished with artificial and natural baits. J. Fish. Biol. 2:155-160.

Beyerle, G.B., and J.E. Williams. 1968. Some observations of food selectivity by northern pike in aquaria. Trans. Amer. Fish. Soc. 97:28-31.

Blest, A.D. 1961. The concept of ritualization, p. 102-124. *In* W.H. Thorpe, and O.L. Zangwill [ed.] Current problems in animal behavior. Cambridge at the University Press, G.B.

Braun, E. 1963. Die ersten Beutefanghandlungen junger Blaufelchen (*Coregonus wartmanni* Bloch) und Hechte (*Esox lucius* L.). Z. Tierpsychol. 20:257-266.

Breder, C.M. Jr. 1959. Studies on social groupings in fishes. Bull. Amer. Mus. Natur. Hist. 117:393-482.

Breder, C.M. Jr. 1967. On the survival value of fish schools. Zoologica (New York) 52: 25-40.

Brett, J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can. 22: 1491-1501.

Brett, J.R. 1970. Fish - The energy cost of living, p. 37-52. In W.J. McNeil [ed.] Marine aquiculture. Oregon State University Press, Eugene, Oregon.

Buss, K. 1961. The northern pike. Special purpose rept., Penn. Fish. Commission, Bonner Spring Fish Research Station. 58 p.

Carlander, K.D. 1969. Handbook of freshwater fishery biology (vol. 1). Iowa State University Press, Ames, Iowa. 752 p.

Carlander, K.D., and E. Cleary. 1949. The daily activity patterns of some freshwater fishes. Am. Midl. Naturalist 41: 447-452.

Casselman, J.M., and H.H. Harvey. 1975. Selective fish mortality resulting from low winter oxygen. Verh. Internat. Verein. Limnol. (Stuttgart) 19: 2418-2429.

Chiszar, D., R.W. Drake, and J.T. Windell. 1975. Aggressive behavior in rainbow trout (Salmo gairdneri Richardson) of two ages. Behav. Biol. 13: 425-431.

Clark, C.F. 1950. Observations on the spawning habits of northern pike, Esox lucius, in northwestern Ohio. Copeia 1950: 285-288.

Clark, C.F., and E.H. Brown, Jr. 1965. Length-weight relationship of northern pike, Esox lucius, from East Harbor, Ohio. Trans. Am. Fish. Soc. 94: 404-405.

Coble, D.W. 1973. Influence of appearance of prey and satiation of predator on food selection by northern pike, Esox lucius. J. Fish. Res. Board Can. 30: 317-320.

Collias, N.E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool. 17: 83-123.

Crook, J.H. 1970. Social organization and environment: aspects of contemporary social ethology. Anim. Behav. 18: 197-209.

Crossman, E.J. 1962. Predator-prey relationships in pikes (Esocidae). J. Fish. Res. Board Can. 19: 979-980.

Davis, G.E., and C.E. Warren. 1968. Estimation of food consumption rates, p. 227-248. *In* W.E. Ricker [ed.] Methods for assessment of fish production in fresh waters. IBP Handbook No. 3, Blackwell Scientific Publications, Oxford, G.B.

Etkin, W. 1967. Social behavior from fish to man. University of Chicago Press, Chicago, Illinois. 204 p.

Erickson, J.G. 1967. Social hierarchy, territoriality, and stress reactions in sunfish. Physiol. Zool. 40: 40-48.

Errington, P.L. 1939. Reactions of muskrats to drought. Ecology 20: 168-186.

Ewing, A.W., and V. Evans. 1973. Studies on the behaviour of cyprinodent fish I. The agonistic and sexual behaviour of *Aphyosemion bivittatum* (Lönnberg 1895). Behaviour 46: 264-278.

Fabricius, E. 1953. Aquarium observations on the spawning behaviour of char, *Salmo alpinus*. Rept. Inst. Freshwater Res. Drottningholm 34: 14-48.

Fabricius, E., and K.J. Gustafson. 1958. Some new observations on the spawning behaviour of the pike, *Esox lucius* L. Rept. Inst. Freshwater Res. Drottningholm 39: 23-54.

Farwell, M.K., and J.M. Green. 1973. Agonistic behavior of juvenile *Stichaeus punctatus* (Pisces: Stichaeidae). Can. J. Zool. 51: 449-456.

Fernet, D.A., and R.J.F. Smith. 1976. Agonistic behavior of captive goldeye (*Hiodon alsoides*). J. Fish. Res. Board Can. 33: 695-702.

Frost, W.E. 1954. The food of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. 23: 339-360.

Frost, W.E., and C. Kipling. 1959. The determination of the age and growth of pike (*Esox lucius* L.) from scales and opercular bones. J. Cons. Perm. Int. Explor. Mer. 24: 314-341.

Frost, W.E., and C. Kipling. 1967. A study of reproduction, early life, weight-length relationship and growth of northern pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. 36: 651-693.

Fortunatova, K.P. 1959. Availability of sticklebacks as food for predacious fishes of the Volga delta. Zool. Zhur. 38: 1689-1701. (Transl. from Russian by Environ. Can. Fish. Mer. Serv. Transl. Ser. No. 331, 1970).

Gerking, S.D. 1953. Evidence for the concepts of home range and territory in stream fish. Ecology 34: 347-365.

Gosline, W.A. 1971. Functional morphology and classification of teleostean fishes. The University Press of Hawii, Honolulu. 208 p.

Gray, J. 1968. How fishes swim, p. 23-29. In N.K. Wessells [ed.] Vertebrate adaptations. W.H. Freeman and Co., San Francisco, California.

Hampton, J.F. 1948. Fighting pike. Salmon and trout magazine 123: 108-109.

Hartman, G.F. 1965. The role of behavior in the ecology and interactions of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 22: 1035-1081.

Healy, A. 1956. Pike (Esox lucius L.) in three Irish lakes. Scient. Proc. R. Dubl. Soc. 27: 51-63.

Hemmings, C.C. 1966. Factors influencing the visibility of objects underwater, p. 359-374. In R. Bainbridge, G.C. Evans, and O. Rackham [ed.] Light as an ecological factor. John Wiley and Sons Inc., New York, N.Y.

Herting, G.E., and A. Witt. 1967. The role of physical fitness of forage fish in relation to their vulnerability to predation by bowfin (Amia calva L.). Trans. Amer. Fish. Soc. 96: 427-430.

Herzog, H.A, and G.M. Burghardt. 1974. Prey movement and predatory behavior of juvenile western yellow-bellied racers, Coluber constrictor mormon. Herpetologica 30: 285-289.

Hinde, R.A. 1966. Animal behavior. McGraw Hill, New York, N.Y. 876 p.

Hoar W.S. 1951. The behavior of chum, pink, and coho salmon in relation to seaward migration. J. Fish. Res. Board Can. 8: 241-263.

Hoogland, R., D. Morris, and N. Tinbergen. 1956. The spines of sticklebacks (Gasterosteus and Pygosteus) as a means of defence against predators (Perca and Esox). Behaviour 10: 205-236.

Hotchkiss, N. 1972. Common marsh, underwater, and floating-leaved plants of the United States and Canada. Dover Publications Inc., New York, N.Y. 124 p.

Humphries, D.A., and P.M. Driver. 1970. Protean defence by prey animals. Oecologia (Berlin) 5: 285-302.

Hunt, R.L. 1965. Food of northern pike in a Wisconsin trout stream. Trans. Amer. Fish. Soc. 94: 95-97.

Ince, B.W., and A. Thorpe. 1976. The effects of starvation and force-feeding on the metabolism of northern pike, Esox lucius L. J. Fish. Biol. 8: 79-88.

Ivanova, M.N. 1969. The behavior of predatory fish during feeding. Problems of Ichthyology 9: 574-577.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Conn., 302 p.

Johnson, L. 1966a. Experimental determination of food consumption of pike, Esox lucius, for growth and maintenance. J. Fish. Res. Board Can. 23: 1495-1505.

Johnson, L. 1966b. Consumption of food by the resident population of pike, Esox lucius, in Lake Windermere. J. Fish. Res. Board Can. 23: 1523-1535.

Johnson, L.D. 1959. The story of a thousand stomachs. Wis. Conserv. Bull. 24: 7-9.

Johnson, L.D. 1969. Food of angler-caught northern pike in Murphy Flowage. Wis. Dept. Natur. Res., Tech. Bull. No. 42: 26 p.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and Salmo trutta L.). Rept. Inst. Freshwater Res., Drottningholm 39: 55-98.

Keenleyside, M.H.A. 1955. Some aspects of the schooling behavior of fish. Behaviour 8: 183-248.

Keenleyside, M.H.A., and F.T. Yamamoto. 1962. Territorial behaviour of juvenile atlantic salmon (Salmo salar L.). Behaviour 19: 139-169.

Kipling, C., and W.E. Frost. 1970. A study of the mortality, population numbers, year class strengths, production, and food consumption of pike, Esox lucius L., in Windermere from 1944 to 1962. J. Anim. Ecol. 39: 115-157.

Lagler, K.F. 1956. The pike, Esox lucius L., in relation to water fowl on the Seney National Wildlife Refuge, Michigan. J. Wildl. Mgmt. 20: 114-124.

Lagler, K.F., J.E. Bardach, and R.R. Miller. 1962. Ichthyology. John Wiley and Sons Inc., New York, N.Y. 545 p.

Lamoureux, R.J. 1973. Environmental impact of hydro on Kakisa Lake, N.W.T. M.Sc. Thesis, Dept. of Zoology, University of Alberta, Edmonton. 260 p.

Lawler, G.H. 1963. The biology and taxonomy of burbot, *Lota lota*, in Heming Lake, Manitoba. J. Fish. Res. Board Can. 20: 417-433.

Lawler, G.H. 1965. The food of the pike, *Esox lucius*, in Heming Lake, Manitoba. J. Fish. Res. Board Can. 22: 1357-1377.

Lawrence, J.M. 1957. Estimated sizes of various forage fishes largemouth bass can swallow. Eleventh Annu. Conf. Southeastern Ass. of Game and Fish Comm. p. 220-225.

Leyhausen, P. 1964. The communal organization of solitary mammals. Symp. Zool. Soc. Lond. 14: 249-263.

Lockie, J.D. 1956. Winter fighting in feeding flocks of rooks, jackdaws, and carrion crows. Bird Study. 3: 180-190.

Lorenz, K.Z. 1950. The comparative method of studying innate behaviour patterns. Symp. Soc. Exp. Biol. 4: 221-268.

Lorenz, K.Z. 1952. King Soloman's ring. Methuen, London. 215 p.

Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes (reproduction and population dynamics) II. Northern pike, *Esox lucius* (Linnaeus). Envir. Can., Fish. Mar. Ser., Tech. Rept. No. 528: 82 p.

Makowecki, R. 1973. The trophy pike, *Esox lucius*, of Seibert Lake. M.Sc. Thesis, Dept. of Zoology, University of Alberta, Edmonton. 239 p.

Malinin, L.K. 1969. Home range and homing instinct in fish. Zool. Zhur. 48: 381-391. (Transl. from Russian by Envir. Can., Fish. Mar. Serv. Transl. Ser. No. 2050, 1973).

Malinin, L.K. 1970. Use of ultrasonic transmitters for tagging bream and pike. Report I. Reaction of fish to net webbing. Biologiya Vnutrennikh Vod. , Informatsionnyi Byulleten 7: 64-69. (Transl. from Russian by Envir. Can., Fish. Mar. Serv. Transl. Ser. No. 1818, 1973).

Malinin, L.K. 1971. Home range and actual paths of fish in the river pool of the Rybinsk Reservoir. Akademiya Nauk SSSR, Institute Biologiya Vnutrennikh Vod., Informatsionnyi Byulleten 22: 158-166. (Transl. from Russian by Envir. Can. Fish. Mar. Serv. Transl. Ser. No. 2282, 1973).

Marler, P. 1956. Studies of fighting in chaffinches: (3) Proximity as a cause of aggression. Brit. J. Anim. Behav. 5: 29-37.

Mauck, W.L., and D.W. Coble. 1971. Vulnerability of some fishes to northern pike (Esox lucius) predation. J. Fish. Res. Board Can. 28: 957-969.

McFarland, D.J. 1965. Hunger, thirst, and displacement pecking in the barbary dove. Anim. Behav. 13: 293-300.

McNamara, F. 1937. Breeding and food habits of the pikes, Esox lucius and Esox vermiculatus. Trans. Amer. Fish. Soc. 66: 372-373.

Miller, R.B. 1948. A note on the movement of the pike, Esox lucius. Copeia 1948: 62.

Miller, R.B., and W.A. Kennedy. 1948. Pike, Esox lucius, from four northern canadian lakes. J. Fish. Res. Board Can. 7: 190-199.

Molnar, G., E. Tamassy, and I. Tolg. 1967. The gastric digestion of living, predatory fish., p. 135-149. In S.D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publ., Oxford, G.B.

Moody, R. 1970. Predation and evolution in sticklebacks. Ph. D. Thesis, Dept. of Zoology, University of Alberta, Edmonton. 88 p.

Morris, D. 1957. 'Typical intensity' and its relationship to the problem of ritualization. Behaviour 11: 156-201.

Morse, D.H. 1974. Niche breadth as a function of social dominance. The American Naturalist 108: 818-830.

Munro, W.R. 1957. The pike of Loch Choin. Freshwat. Salm. Fish. Res. 16: 1-16.

Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London, G.B. 352 p. (Transl. by L. Birkett).

Nursall, J.R. 1973. Some behavioral interactions of spottail shiners (Notropis hudsonius), yellow perch (Perca flavescens), and northern pike (Esox lucius). J. Fish. Res. Board Can. 30: 1161-1178.

Paetz, M.J., and J.S. Nelson. 1970. The fishes of Alberta. The Queen's Printer, Edmonton, Alberta. 282 p.

Pennak, R.W. 1953. Fresh-water invertebrates of the United States. The Ronald Press Co., New York, N.Y. 769 p.

Poddubnyi, A.G., L.K. Malinin, and V.V. Gaiduk. 1970. Experiment in telemetric observations under ice of the behaviour of wintering fish. Biologiya Vnutrennikh Vod. Informatsionnyi Byulleten 6: 65-70. (Transl. from Russian by Envir. Can., Fish. Mar. Serv. Transl. Ser. No. 1817, 1972).

Popova, O.A. 1967. The 'predator-prey' relationship among fishes (a survey of soviet papers), p. 359-376. In S.D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, G.B.

Qadri, S.U. 1960. A small drag-net for the capture of bottom fish and invertebrates. Prog. Fish Cult. 22: 90-92.

Roberts, W.E. 1975. Food and space utilization by the piscivorous fish of Cold Lake, with emphasis on introduced coho salmon. M.Sc. Thesis, Dept. of Zoology, University of Alberta, Edmonton. 160 p.

Sale, P.F. 1972. Effect of cover on agonistic behavior of reef fish: a possible spacing mechanism. Ecology 53: 753-758.

Schoener, T.W. 1967. The ecological significance of sexual dimorphism in size in the lizard Anolis conspersus. Science 155: 474-476.

Schoener, T.W. 1969. Models of optimal size for solitary predators. American Naturalist 103: 277-313.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Seaburg, K.G., and J.B. Moyle. 1964. Feeding habits, digestion rates, and growth of some Minnesota warmwater fishes. Trans. Amer. Fish. Soc. 93: 269-285.

Selye, H. 1949. Textbook of endocrinology. 2nd ed. Acta Endocrinologica, Montreal. 914 p.

Selye, H. 1961. Nonspecific resistance. Ergeb. Pathol. 41: 208-241.

Slaney, P.A., and T.G. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (Salmo gairdneri) in laboratory stream channels. J. Fish. Res. Board Can. 31: 1201-1209.

Slobodkin, L.B. 1968. How to be a predator. Amer. Zoologist 8: 43-51.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames. 593 p.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Co., San Francisco, Calif. 776 p.

Solman, V.E.F. 1945. The ecological relations of pike, Esox lucius L., and waterfowl. Ecology 26: 157-170.

Springer, S. 1967. Social organization in shark populations, p. 149-174. In P.W. Gilbert, R.F. Mathewson, and D.P. Rall [ed.] Sharks, skates, and rays. Johns Hopkins Press, Baltimore, Maryland.

Stokes, A.W. 1962. Agonistic behavior of blue tits at a winter feeding station. Behaviour 19: 118-138.

Svardson, F. 1948. Note on spawning habits of Leuciscus erythropthalmus (L.), Abramis brama (L.), and Esox lucius L. Rept. Inst. Freshwater Res. Drottningholm 29: 115-122.

Swift, D.R. 1955. Seasonal variation in the growth rate, thyroid gland activity, and food reserves of brown trout (Salmo trutta L.). J. Exp. Biol. 32: 751-764.

Tatsumi, U. 1972. Social facilitation in feeding behavior of the guppy: II. Experimental analysis of mechanisms. Jap. J. Ecol. 21: 54-67.

Thomas, G. 1974. The influences of encountering a food object on subsequent searching behavior in Gasterosteus aculeatus L. Anim. Behav. 22: 941-952.

Tinbergen, N. 1952. 'Derived' activities; their causation, biological significance, origin, and emancipation during evolution. Q. Rev. Biol. 27: 1-32.

Tinbergen, N. 1957. The functions of territory. Bird Study 4: 14-27.

Tinbergen, N., M. Impekoven, and D. Franck. 1967. An experiment on spacing-out as a defence against predation. Behaviour 28: 307-321.

Toner, E.D., and G.H. Lawler. 1969. Synopsis of biological data on the pike, Esox lucius (Linnaeus 1758). F.A.O. Fish. Synops. 30 Rev. I.: 37 p.

Ward, H.B., and G.C. Whipple. 1959. Freshwater Biology. W.T. Edmondson [ed.], 2nd ed. John Wiley and Sons Inc., New York, N.Y. 1248 p.

Wich, K. 1958. A compendium of the life history and ecology of the chain pickerel, Esox niger (LeSueur). Massachusetts Div. of Fish. and Game, Fisheries Bull. 22: 27 p.

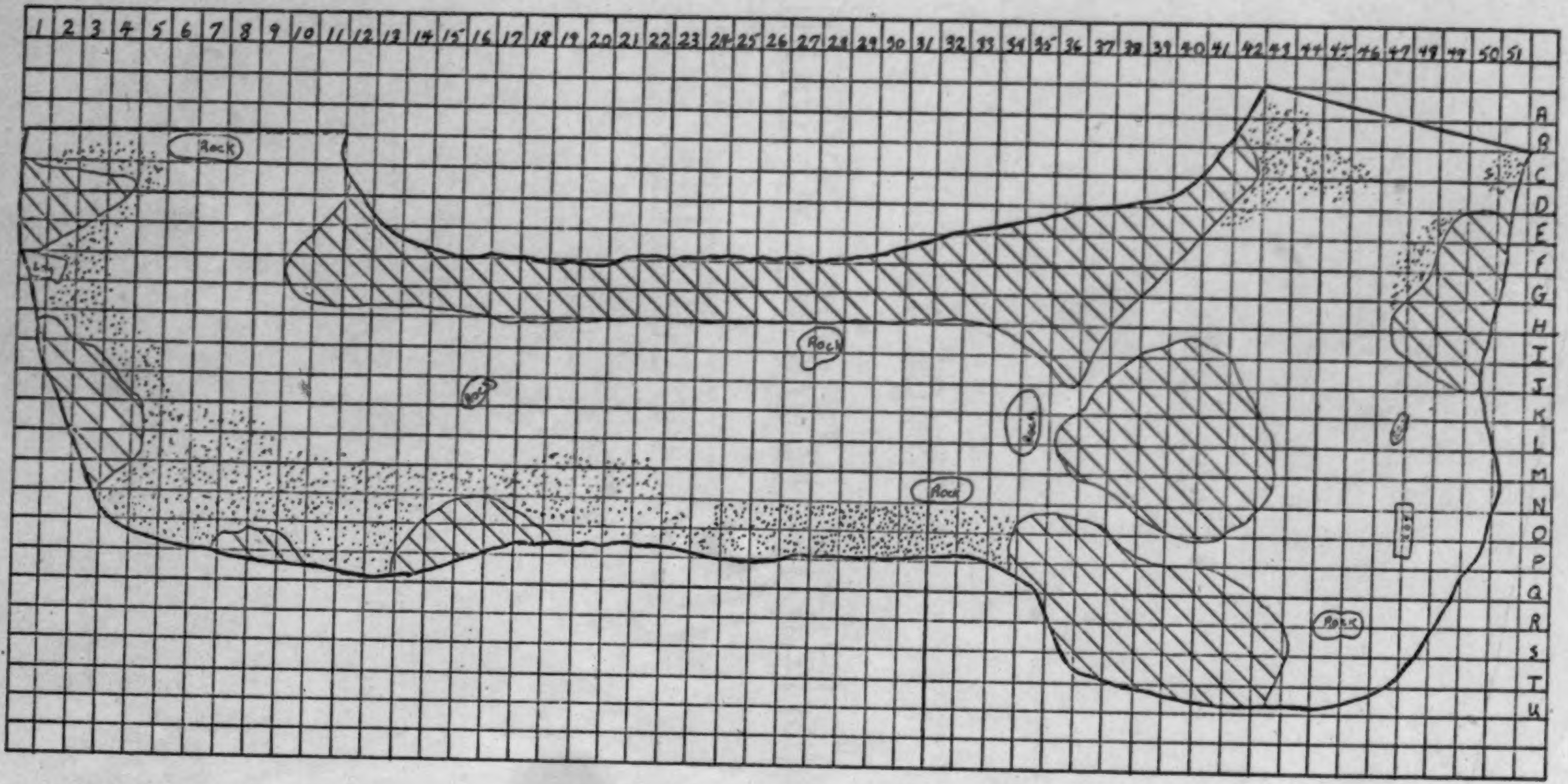
Wunder, W. 1927. Synnesphysiologische Untersuchengen über die Nahrungsaufnahme verschiedener Knochenfischarten. Z. vergl. Physiol. 6: 67-98. Cited in E.D. Toner, and G.H. Lawler. 1969. Synopsis of biological data on the pike, Esox lucius (Linnaeus 1758). F.A.O. Fish. Synops. 30 Rev. I.: 37 p.

Wynne-Edwards, V.C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburg. 653 p.

Zack, S. 1974. Sequences of agonistic behavior patterns and food deprivation in Hermissenda. Behav. Biol. 12: 525-532.

APPENDIX 1. Fish species collected from Kakisa Lake. Estimated relative abundance is greater for those species having higher number of asterisks.

Fish Species		Relative Abundance
Spottail shiner	*Notropis hudsonius* (Clinton)	*****
Cisco	*Coregonus artedii* Lesueur	****
Lake whitefish	*Coregonus clupeaformis* (Mitchill)	***
Northern pike	*Esox lucius* L.	***
Trout-perch	*Percopsis omiscomaycus* (Walbaum)	***
Ninespine stickleback	*Pungitius pungitius* (L.)	***
Walleye	*Stizostedion vitreum* (Mitchill)	***
Lake chub	*Couesius plumbeus* (Agassiz)	**
White sucker	*Catostomus commersoni* (Lacepede)	**
Round whitefish	*Prosopium cylindraceum* (Pallas)	*
Burbot	*Lota lota* (L.)	*
Longnose sucker	*Catostomus catostomus* (Forster)	*
Slimy sculpin	*Cottus cognatus* Richardson	*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APPENDIX 2. Map of Study Stream observation area, with alphanumeric coordinate grid system used to locate exact fish positions.

APPENDIX 3. Limnological parameters: a comparison between the Study Stream (SS), Muskeg River (MR), and Kakisa Lake (KL). All values, except pH, in mg./1. . Abbreviation- Alk = Alkalinity.

Date and Area	pH	O_2	Total Alk as $CaCO_3$	Ortho Phosphate	Nitrate	Total Dissolved Solids	Total $CaCO_3$ Hardness
June 2/73							
SS		5.6					
MR		7.7					
June 16/73							
SS		7.3					
MR		7.9					
KL		9.2					
July 4/73							
SS	9.2	8.7	142.2	0.04	0.32	835.0	548
MR	9.2	9.9	126.6	0.04	0.03	260.5	164
KL	8.5	8.2	70.5	0.03	0.05	140.4	116
July 30/73							
SS	8.5	9.1	172.0	0.05	0.09	702.1	436
MR	8.5	7.6	105.0	0.05	0.08	158.2	144
KL	8.3	7.7	91.6	0.04	0.05	165.8	112
Aug 13/73							
SS	8.1	7.6	134.5	0.08	0.11	446.8	316
MR	8.7	8.5	133.0	0.11	0.08	270.9	180
KL	7.9	9.2	86.5	0.15	0.03	230.5	132

APPENDIX 3. (con'd)

Date and Area	pH	O_2	Total Alk as $CaCO_3$	Ortho Phosphate	Nitrate	Total Dissolved Solids	Total $CaCO_3$ Hardness
May 3/74							
SS	7.4	7.2	53.0	0.06	0.09	586.0	340
MR	8.0	8.3	56.0	0.10	0.07	217.4	140
May 27/74							
SS	7.8	7.1	75.0	0.05	0.10	719.2	460
MR	8.0	8.1	56.0	0.10	0.07	217.4	140
KL	8.0	8.6	84.2	0.04	0.02	214.6	124
June 20/74							
SS	8.7	5.2	108.0	0.08	0.09	223.7	184
MR	8.5	7.4	104.6	0.04	0.07	273.5	160
KL	8.6	8.8	75.0	0.05	0.04	169.2	116
July 10/74							
SS	8.2	6.4	111.0	0.16	0.09	466.6	332
MR	8.4	6.9	117.4	0.05	0.08	260.0	168
LK	8.4	9.9	82.0	0.05	0.04	153.0	120
Aug 1/74							
SS	8.6	6.0	139.2	0.05	0.07	423.6	284
MR	8.8	7.0	136.0	0.05	0.03	221.3	184
KL	8.2	9.7	73.0	0.04	0.04	105.7	120

APPENDIX 4. Invertebrate food of northern pike between 20 and 70 cm fork length.

Invertebrates occurring in stomachs of northern pike	Number of pike containing	Percent of total pike examined	Percent occurrence in feeders	Total number of invertebrates	Mean number per fish
Hirudinea *Dina* *Haemopsis* *Macrobdella*	26	4.1	7.5	46	1.8
Amphipoda *G. lacustris* *H. azteca*	86	13.4	25.1	1718	20.0
Ephemeroptera *Ephemera* *Hexagenia*	40	6.2	11.7	96	2.4
Odonata *Ischnura* *Aechna* *Libellula* *Somatochlora* *Sympetrum*	52	8.1	15.2	210	4.0
Megaloptera *Sialis*	1	0.2	0.3	1	1.0
Trichoptera *Banksiola* *Phryganea* *Hydropsyche* *Heliopsyche*	30	4.7	8.7	45	1.5
Coleoptera *Dytiscus* *Haliplus*	7	1.1	2.0	8	1.1
Diptera *Chironomus* *Simulium* *Chaoborus*	16	2.5	4.7	34	2.1
Gastropoda *Valvata* *Physa*	13	2.0	3.8	28	2.2